

Three new morphologically and genetically determined species of hydrobiid gastropods from Dalhousie Springs, northern South Australia, with the description of a new genus

W. F. Ponder, D. J. Colgan, T. Terzis,
S. A. Clark and A. C. Miller

Australian Museum
6 College Street, Sydney, New South Wales 2000

A new genus (*Dalhousia*) containing two new species (*D. globosa* and *D. harrisi*), and a new species of *Fluvidona* (*F. centralia*) are described from Dalhousie Springs in northern South Australia. Allozyme data from 77 populations are presented and used to justify the separation of the two species. *Dalhousia* is the sister group of *Fonscochlea* from the Lake Eyre Supergroup springs but differs from that genus in females having a single sperm pouch. Species of *Fluvidona* are otherwise found in streams and rivers, mainly in south eastern Australia, *F. centralia* being the only species known from central Australia. The anatomy of the three species is described and a summary of their variation, based on shell measurements and allozymes, is presented.

Introduction

There are many artesian springs associated with the Great Artesian Basin (GAB) in South Australia (Ponder, 1986; Boyd, 1990) and they are of great interest, biologically, limnologically and geologically. Their considerable conservation significance has been recognised (Harris, 1981, 1993; Ponder, 1985, 1986, 1995; DEST, 1994).

Two major groups of artesian springs are associated with the section of the GAB in South Australia. The largest group, the Lake Eyre Supergroup (Habermehl, 1982; Ponder, 1986), lies in a line running roughly south west between Marree and Oodnadatta. The other major group, Dalhousie Springs, comprises approximately 80 springs in a small area (about 70 km²) of far northern South Australia which together have the largest natural discharge of water from the GAB (Habermehl, 1982; Smith, 1989). Aspects of their history, biology, limnology and geology are described in Zeidler & Ponder (1989). The springs contain a number of endemic aquatic animals, including fishes (Glover, 1989; Crowley & Ivantsoff, 1990), amphipods (Zeidler, 1989, 1991) and hydrobiid gastropods (Ponder, 1989 and herein). The latter are by far the most abundant and conspicuous of the endemic aquatic invertebrates, as is the case in other GAB artesian springs (see below) and also in some spring systems in the Americas (e.g. Hershler, 1985; Hershler and Landye, 1988; Hershler and Sada, 1987). These snails are generally associated with long-term permanent water (Ponder, 1994).

A study on the hydrobiid snails of the Lake Eyre Supergroup springs demonstrated considerable morphological and genetic diversity (Ponder *et al.*, 1989; in press) and hydrobiids from springs associated with the Queensland part of the GAB have been described by Ponder and Clark (1990).

A major survey of Dalhousie Springs was undertaken in 1985, the results presented in Zeidler and Ponder (1989). In a review of the aquatic molluscs of Dalhousie, Ponder (1989) recognised an undescribed fauna of "at least six species of hydrobiid snails" based on gross shell differences, but noted the extremely variable shell morphology encountered in the springs. Major differences in shell size and shape were noted between populations inhabiting different environments, even associated with a single spring. Preliminary morphological analysis indicated that standard techniques were not able to distinguish putative taxa. A second major survey of the fauna was undertaken in 1990 to

collect material for electrophoretic examination. In all, 77 samples were subsequently analysed. These results, combined with an analysis of shell measurement data for most of these samples, are presented here. Aspects of the genetic results obtained from the Dalhousie samples, particularly relating to gene flow, have been published elsewhere (Colgan and Ponder, 1994).

In this paper three taxa are described, two congeners (the common snails found in the springs) are separated using allozyme differences, and a third is a member of a separate genus (*Fluvidona*) and is restricted to a few small seepages and cold outflows.

Material and methods

Collection. Material was collected by hand from many springs and each collection site for the

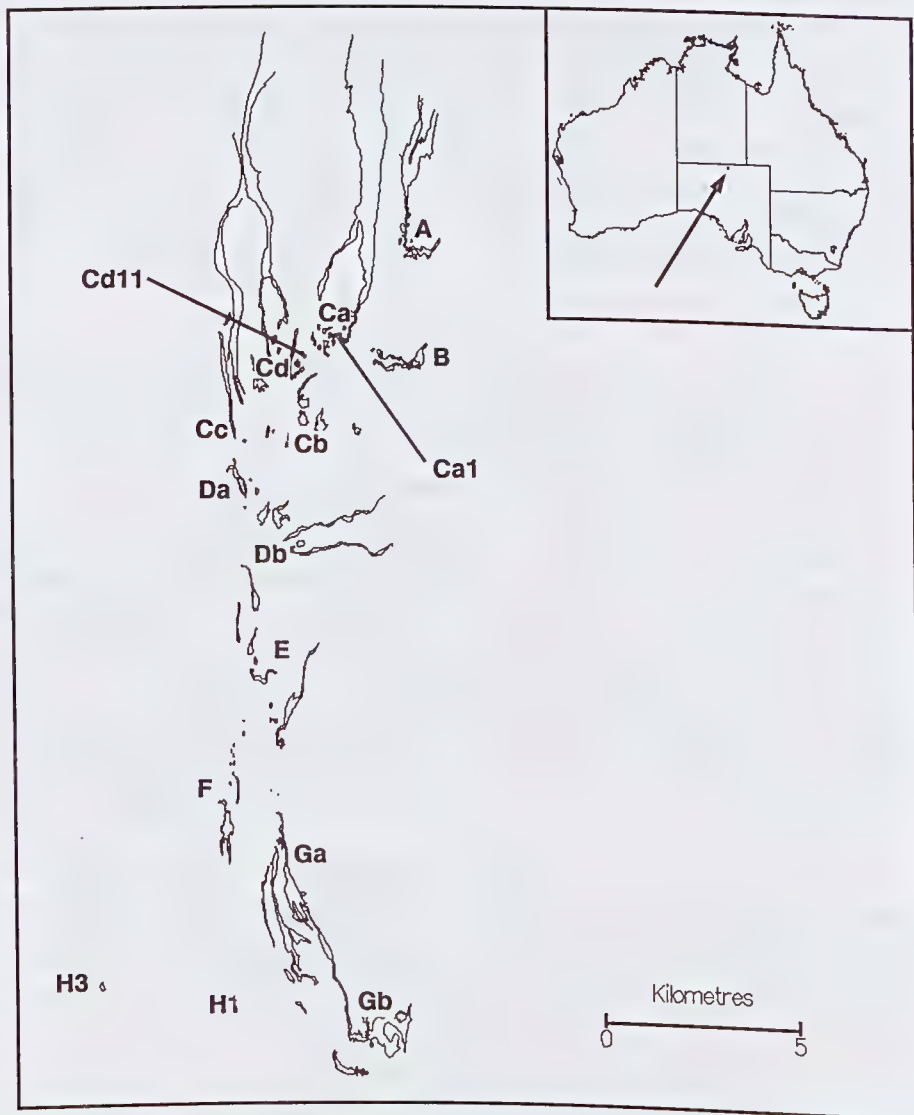


Figure 1. Map of Dalhousie Springs showing the springs from which samples were obtained for this study.

material used in the genetic analysis is listed in Appendix 1 (see also Ponder, 1989 for overall locality details). Latitudes and longitudes have been calculated using a GIS system (MapInfo ver. 5.01; Mapping Information Systems, 1985–1991), after digitizing the spring details based on the locality map in Zeidler and Ponder (1989, fig. 2). The spring numbers used follow Zeidler and Ponder (1989) and are shown in Fig. 1.

Morphology studies. Dissection and preparation of material for SEM were by standard methods (Ponder *et al.*, 1993). Morphological observations presented here for the three new species are based on the type populations. The majority of populations have also been examined in less detail to confirm the main anatomical characters and a summary of their shell measurements and ratios are presented (Appendix 2).

Shell measurements were obtained using the methods described by Ponder *et al.* (1989), those parameters measured being listed below. The number of opercular pegs was counted only in the species of *Fluvidona*, those in the new genus being too ill-formed in many specimens to count accurately. In the statistics given in each description male and female shell measurements have been pooled and the range of morphology taken from the total pool of data available for that locality. These are given separately in the measurement tables presented for each type lot and in Appendix 2 (Tables 2 and 3). Statistical analysis was performed using SYSTAT (Wilkinson, 1992). Material is held in the South Australian Museum, Adelaide (SAM) and the Australian Museum, Sydney (AMS).

Abbreviations used in tables of measurements:

AL – shell aperture length; AW – shell aperture width; BW – length of last (body) whorl of shell; CV – convexity ratio of penultimate whorl of shell; OL – length of operculum; OS – length of white opercular smear; OW – width of operculum; PH – height of longest opercular peg; PL – length of area occupied by opercular pegs; PN – number of opercular pegs; SL – shell length; SW – shell width; TW – number of teleoconch whorls.

Electrophoresis. Standard methods for cellulose acetate electrophoresis were used (Richardson *et al.*, 1986; Hebert and Beaton, 1989; Ponder *et al.*, 1991). Snails were homogenized in about 20 µl (10 µl for small individuals) of buffer, providing enough sample for up to 12 gels. Where more than one locus encoding the same enzyme was found, they were designated numerically in order of decreasing mobility. Allozymes identified for each locus within a species are designated in the same way. The enzymes scored for each species, together with abbreviations, Enzyme Commission Numbers, and the number of loci are listed in Table 1. The computer package BIOSYS-1 (Swofford and Selander, 1989) was used to assist analysis.

Table 1. The numbers of interpretable loci. The columns give the enzyme name, its abbreviation, E.C. number and the number of interpretable loci for: A, *Dalhousia* spp.; and B, *Fluvidona*.

ENZYME	ABBREVIATION	E.C. NO.	A	B
Alcohol dehydrogenase	ADH	1.1.1.1	1	
Alkaline phosphatase	ALKP	3.1.3.1	1	1
Aspartate aminotransferase	AAT	2.6.1.1	2	2
Enolase	ENO	4.2.1.11	1	1
Esterase	EST	3.1.1.1	3	3
Fumarate hydratase	FH	4.2.1.2	1	
β-Galactosidase	GAL	3.2.1.23	1	
Glycerol-3-phosphate dehyd.	GPD	1.1.1.8	1	1
Glucosephosphate isomerase	GPI	5.3.1.9	1	1
Glutamate-pyruvate transamin.	GPT	2.6.1.2	1	
Hexokinase	HK	2.7.1.1	1	
Hydroxybutyrate dehydrogenase	HBDH	1.1.1.30	1	
Isocitrate dehydrogenase	IDH	1.1.1.42	2	2
Leucine aminopeptidase	LAP	3.4.11	1	
Malate dehydrogenase	MDH	1.1.1.37	2	2

Mannosephosphate isomerase	MPI	5.3.1.8	1	1
Peptidases: Phe-Pro substrate	PPR	3.4.11	1	1
: Leu-Ala substrate	LAL	3.4.11	1	
: Leu-Leu-Gly substrate	LGG	3.4.11	2	
Phosphoglucomutase	PGM	5.4.2.2	2	2
6-Phosphogluconate dehydrog.	6-PGDH	1.1.1.44	1	1
Sorbitol dehydrogenase	SDH	1.1.1.14	2	2
Triosephosphate isomerase	TPI	5.3.1.1	1	1
UDP glucose pyrophosphorylase	UDPG	2.7.7.9	1	1

Results

Taxonomy

Three new species in two genera, one new, are described below, as are the electrophoretic results confirming the status of these species.

Dalhousia n. gen.

Type species: *Dalhousia globosa* n. sp.

Diagnosis: Hydrobiids with simple, smooth, imperforate, broadly ovate to conic shell, with simple aperture and lacking external varix. Operculum with weakly to moderately-developed pegs on inner side and radula with two laterally placed basal cusps on central teeth. Female genital system with single globular, posteriorly-located medium-sized sperm sac and posteriorly elongated coiled oviduct. Male with long, tapering (whip-like) penis. Stomach with horn-like process on upper edge of posterior chamber and lacking obvious caecum.

Description: Shell (Figs 2A-C, F-H, 3-5) simple, smooth, imperforate, broadly ovate to conic, with simple oval aperture and lacking external varix. Protoconch (Fig. 6A,B) of about 1.5 whorls, sculptured with irregular, shallow pits. Operculum (Fig. 7A-E) thin, flat, with white smear and weakly to moderately-developed pegs on inner side. Body heavily pigmented (mainly black), cephalic tentacles with narrow, median-dorsal unpigmented line (corresponding to line of dorsal cilia) and narrow unpigmented zone at base of tentacles. Mid-dorsal strip of cilia rather weakly-developed and set in a narrow, shallow groove (Fig. 8B,C); three more strongly developed ciliary strips ventrally, two ventro-lateral and one mid-ventral (Fig. 8A,B). Snout (Fig. 9A-D) with little or no cilia dorsally, some ciliary tufts latero-ventrally. Labial area weakly papillate, papillae with very short cilia-like processes (Fig. 9D).

Anatomy generally similar to *Fonscochlea* (Ponder *et al.*, 1989). Columellar muscle short and wide. Ctenidium large, with numerous broadly triangular filaments, posterior end usually slightly overlapping anterior edge of pericardium. Osphradium oval, short, behind middle of ctenidium. Hypobranchial gland very narrow, weakly to moderately developed. Rectum straight or slightly arched in pallial cavity, with longitudinally orientated faecal pellets and, usually, partially overlapping pallial oviduct glands. Radula (Fig. 10) with 2 pairs of basal cusps on central teeth, otherwise typical of family. Stomach (Fig. 11) with characteristic "horn"-like process on upper edge of posterior chamber with caecum rudimentary or absent. Renal organ protruding partly into pallial roof, renal opening usually with white lips, renal gland longer than wide. Prostate gland (Fig. 12A,B) broadly oval, much higher (*i.e.* dorso-ventral dimension) than thick, mostly visceral, with pallial vas deferens opening near posterior pallial wall. Penis (Figs 12C, 13) long, tapering, whip-like, with pointed distal end. Penial duct (Fig. 12C) undulating in small, moderately expanded basal section, straight in long distal part. Female reproductive system similar to *Fonscochlea* but with only a single globular sperm sac (Fig. 14, sps). Coiled oviduct (Fig. 14A,B, co) with simple, U-shaped proximal part, long posterior extension, wrapped around sperm sac in S-shaped coil; proximal part



Figure 2. Shells of *Dalhousia* species and *Fluvidona centralia*. A-C.F.G. *D. harrisi*. A, holotype; B, paratype; C, Spring Ca13A; F,G, Spring Ca7 (station C643). D,E. *F. centralia*. D, holotype; E, lower outflow of Spring E1 (station D62). H, *D. globosa*, holotype. Scales 0.5mm.

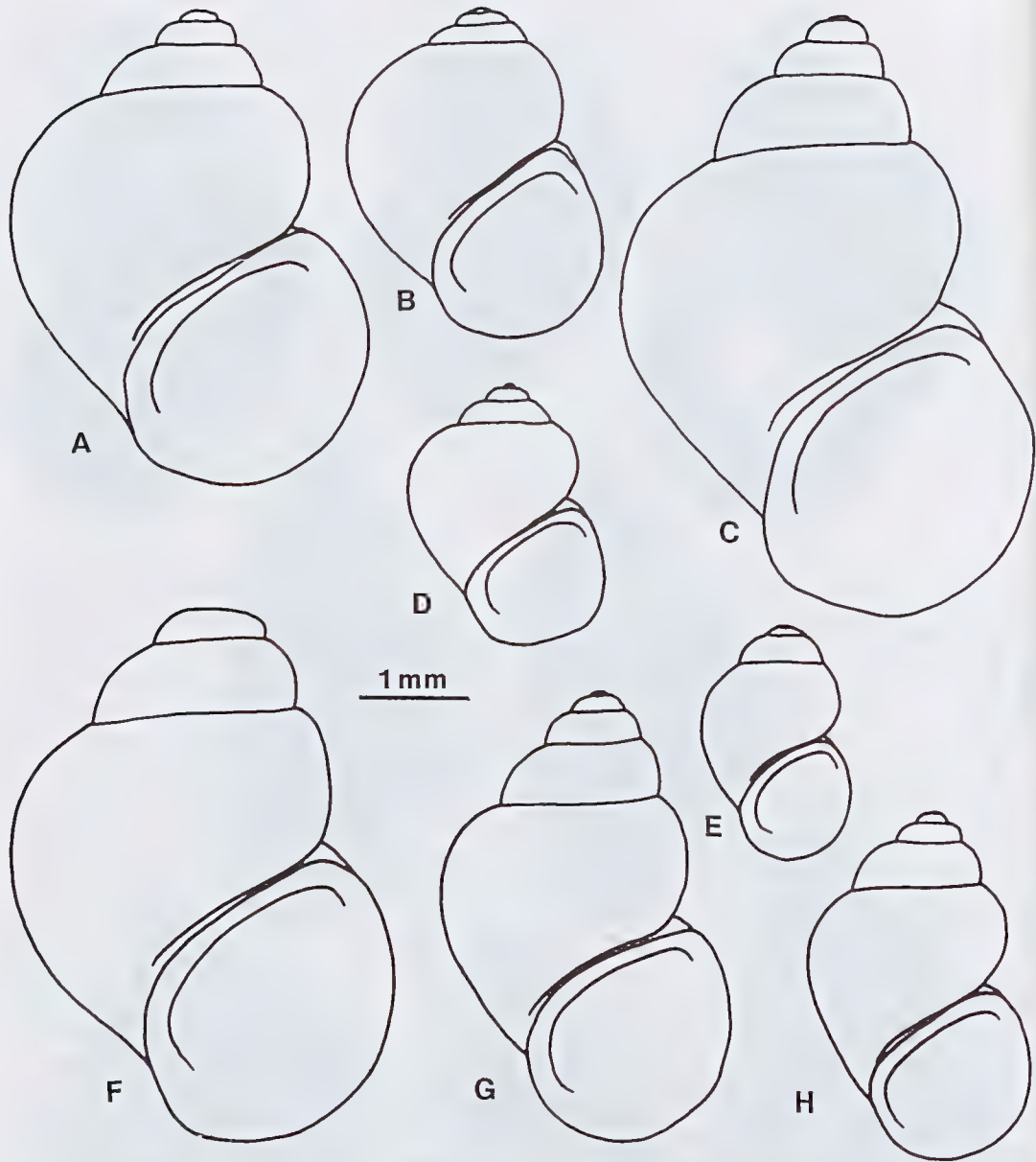


Figure 3. Shells of *Dalhousia globosa*. A. Spring Ca1 (station D26), B. Spring Ca1 (station D46), C, D. Spring Cd1 (station D43), E, H. Spring Ca1a (station D24), F. Spring A1 (station D4A), G. Spring Cb2 (station D51).

of this duct containing stored sperm (Fig. 14C,D, sp); duct to sperm sac very short. Common duct (Fig. 14, cd) very long. Pallial oviduct simple, with or without distinct glandular zones, opening small, terminal (Fig. 14A,B, po). Nervous system typical of family, with long supra-oesophageal connective and suboesophageal ganglion abutting left pleural ganglion.

Remarks. The anatomy of the new genus is generally similar to that described in detail for other Australian hydrobiids (*Fonscochlea* Ponder *et al.*, 1989; *Tatea* Ponder *et al.*, 1991; and *Fluvidona*

Ponder *et al.*, 1994). However, *Dalhousia* differs from these genera, and other hydrobiid genera, in the combination of characters listed in the diagnosis. Most similar to *Fonscochlea*, the new genus can be readily distinguished by its apomorphic single sperm sac and very elongate penis. When superimposed on the cladogram produced by Ponder and Clark (1990) *Dalhousia* is the sister taxon to *Fonscochlea*.

Dalhousia globosa n. sp.

Figs 2H, 3, 6A,B, 7A,B, 8C, 9A, 10B–D,F, 11B, 12A,C, 13A, 14A,C, 16A,C,D, 22, 23, 24.

Ponder, 1989, figs 11.1F, 11.2B,C,G.

Etymology. *Globosa* – globus, globulus, Latin – ball, sphere.

Type locality. Ca1, the main spring (Earwanyera Spring), Dalhousie Springs, South Australia.

Collection details of type material. Stn. C641B–C, Spring Ca1, 26°24'29"S 135°31'08"E, on rocks & wood from shallow water. 28/5/1983, Coll. W. Ponder & W. Zeidler.

Holotype, SAM, D18937, paratypes, SAM, 18938, AMS, C.201743(C641B), C.201750(C641C).

Diagnosis: Typically with large, globose shell. Distinguished electrophoretically from the next species in having very high frequencies of the LAP 2, PGM–2 3, SDH–1 1 and SDH–2 2 allozymes, and a high frequency of the GPI 2 allozyme.

Description: Shell (Fig. 2H, 3). Shell opaque, small (1.7–4.6 mm in length, mean in type series 4.1), broadly conical to globose, SW/SL 0.67–0.97 (overall mean 0.79, 0.77 in type series), AL/SL 0.46–0.69 (mean 0.55), sutures impressed, whorls usually narrowly shouldered. Protoconch (Fig. 6A,B) of about 1.5–1.6 whorls, minutely punctate. Teleoconch of 2.8–4.2 (mean 3.3) strongly convex whorls, sutures impressed; sculpture of indistinct growth lines only. Aperture slightly longer than wide, AW/AL 0.78–1.06 (mean 0.92, 0.94 in type series), angled posteriorly. Peristome with sharp edge, moderately thickened internally, entire, with inner lip attached to parietal wall. Colour (imparted by periostracum) pale yellow to yellow-brown. There is no significant sexual dimorphism in shell size in the type population.

Dimensions of holotype.

	SL	SW	AL	AW	BW	TW
Holotype	4.16	3.35	2.36	2.06	3.45	3.2

Dimensions of specimens from paratype series

Female, N=13

	SL	SW	AL	AW	BW	CV	TW
Minimum	3.61	2.97	2.08	1.93	3.10	0.18	3.0
Maximum	4.52	3.52	2.42	2.23	3.61	0.26	4.2
Mean	4.11	3.20	2.21	2.08	3.43	0.23	3.3
S.D.	0.25	0.18	0.11	0.10	0.16	0.02	0.34

Male, N=7

	SL	SW	AL	AW	BW	CV	TW
Minimum	3.57	2.86	1.96	1.90	3.09	0.20	2.75
Maximum	4.61	3.30	2.43	2.17	3.73	0.25	3.50
Mean	4.09	3.09	2.19	2.04	3.42	0.23	3.21
S.D.	0.38	0.17	0.19	0.09	0.23	0.02	0.25

Summarised shell dimensions of an additional 200 specimens from various points within Spring

Ca1 are given in Appendix 2. Note that the mean size is considerably smaller than those of the pool population (Fig. 16C).

Operculum (Fig. 7A,B). Ovate, thin, pale yellow, with eccentric nucleus, usually with 4–5 small, weak pegs on white smear on inner side.

Statistics of 20 opercula from the type series.

Female, N=13

	OL	OW	OS	PL	PH
Minimum	1.55	1.13	0.44	0.10	0.05
Maximum	1.79	1.36	0.86	0.48	0.15
Mean	1.69	1.28	0.65	0.34	0.09
S.D.	0.07	0.07	0.13	0.09	0.03

Male N=7

	OL	OW	OS	PL	PH
Minimum	1.56	1.17	0.42	0.23	0.06
Maximum	1.80	1.35	0.73	0.49	0.13
Mean	1.68	1.25	0.58	0.36	0.09
S.D.	0.11	0.08	0.10	0.09	0.03

Radula (Fig. 10B–D,F). Central teeth broad, each with 3–4 (usually 4) small, triangular cusps on either side of a sharp median cusp about twice the length of the adjacent cusps. Two pairs of lateral basal denticles present, innermost larger. Lateral teeth with largest cusps in tooth row, 3–4 on inner side of large triangular median cusp and 3–4 (usually 3) on outer side. Inner marginal teeth with 20+ sharp cusps (approx. half length of those on inner marginal teeth) on antero-distal and inner-distal edge. Outer marginal teeth with small, narrow, sharp cusps (approx. half length of those on inner marginal teeth) on antero-distal and inner-distal edge.

Head-foot. Cephalic tentacles pigmented dorsally, with narrow unpigmented mid-dorsal stripe; snout and dorsal neck also pigmented. Ciliation (Figs 8C, 9A) as for generic description. Foot, and especially opercular lobes, weakly pigmented; pallial roof and visceral coil variable but usually black or mottled with grey or black.

Anatomy. Osphradium unpigmented, located at posterior quarter of ctenidium, narrowly oval, 0.27–0.42 mm in length. Ctenidium with 30–37 broadly triangular filaments, apices central to towards right; maximum width 0.46–0.76 mm, posterior 2–3 filaments overlapping pericardium. Rectum straight in pallial cavity in both sexes. Renal organ extending 1/3 (rarely 1/4) length of renal gland into pallial roof; renal gland 0.65–0.92 mm in length, 0.32–0.43 mm in width. Pericardium length, stomach proper 0.77–0.89 mm in length, caecum absent or rudimentary. Stomach (Fig. 11B) with style sac 0.76–0.92 mm in length, stomach proper 0.77–0.89 mm in length, caecum absent or rudimentary.

Testis of 1.8–2.0 whorls; seminal vesicle visible externally and lies between digestive gland and testis for only 0.2–0.3 whorls behind stomach, convolute over stomach. Prostate gland (Fig. 12A) 0.54–0.62 mm in length (about 0.06–0.15 mm in pallial roof), 0.35–0.48 mm in height, broadly oval, narrowly oval in section. Pallial vas deferens coiled, forming densely pigmented (grey to black – darker than surrounding epithelium of neck) low, rope-like ridge across neck at base of penis; with few undulations nearer prostate, straight immediately anterior to, and beneath, prostate. Penis (Figs 12C, 13A) unpigmented or with proximal part of distal section of penis with grey pigmentation, basal section unpigmented or with some grey pigment; distal section long and evenly tapering, basal section relatively small, expanded. Penis base 0.37–0.49 mm from right eye, just to right of midline.

Ovary of 1.1–1.2 whorls. Coiled oviduct (Fig. 14A,C, co) with 1 distal U-shaped loop, orientated anteriorly; distal part straight, posteriorly wrapped around sperm sac (Fig. 14A, sps) in S-shape coil. Duct to sperm sac ventral, very short (virtually direct communication). Common duct (Fig. 14A,C,

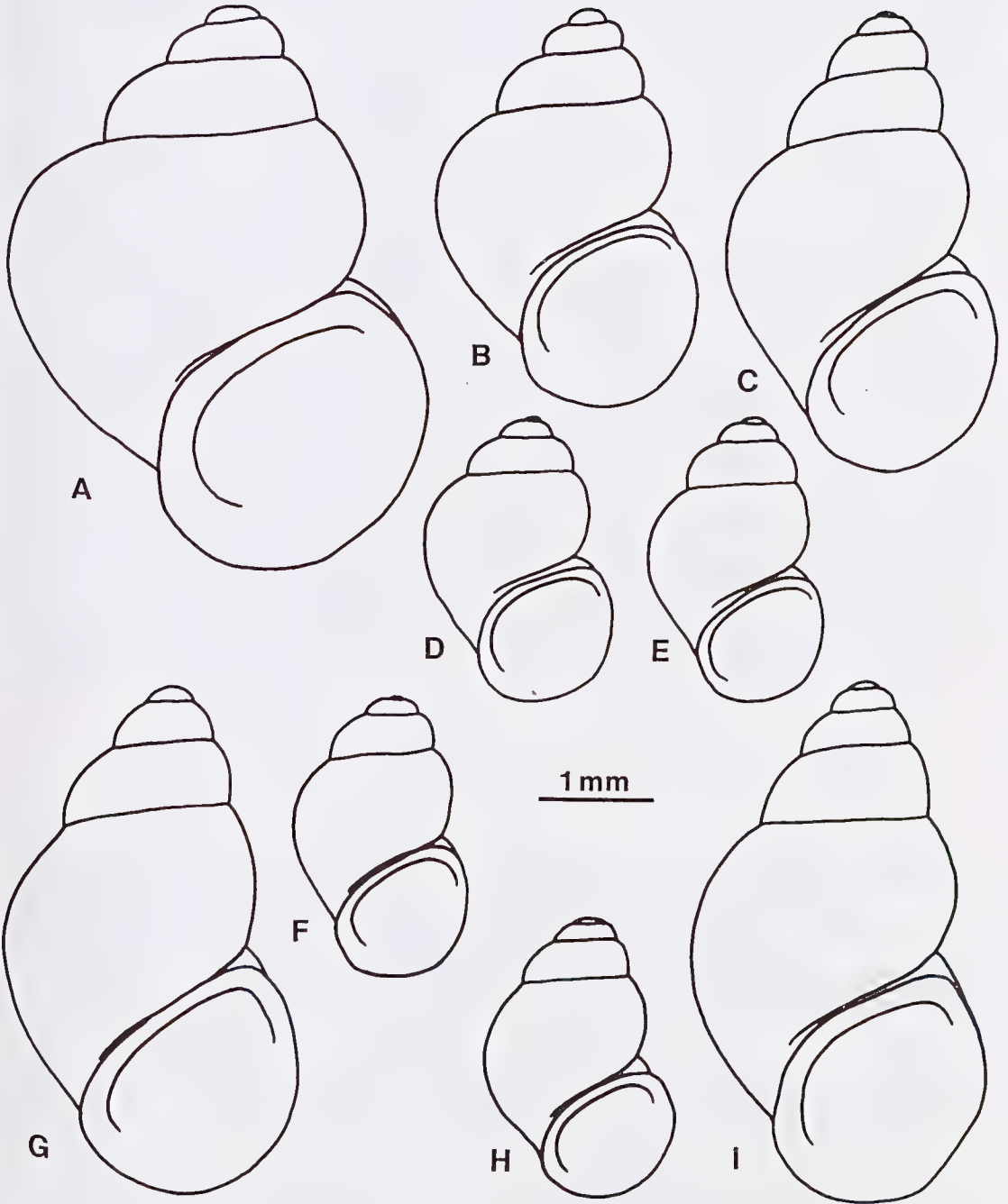


Figure 4. Shells of *Dalhousia harrisi*. A, B, D. Spring Ca5 (station D75), C, E. Spring Db2 (station D20), F, G. Spring Ga6B (station D16), H, I. Spring F1 (station D54).

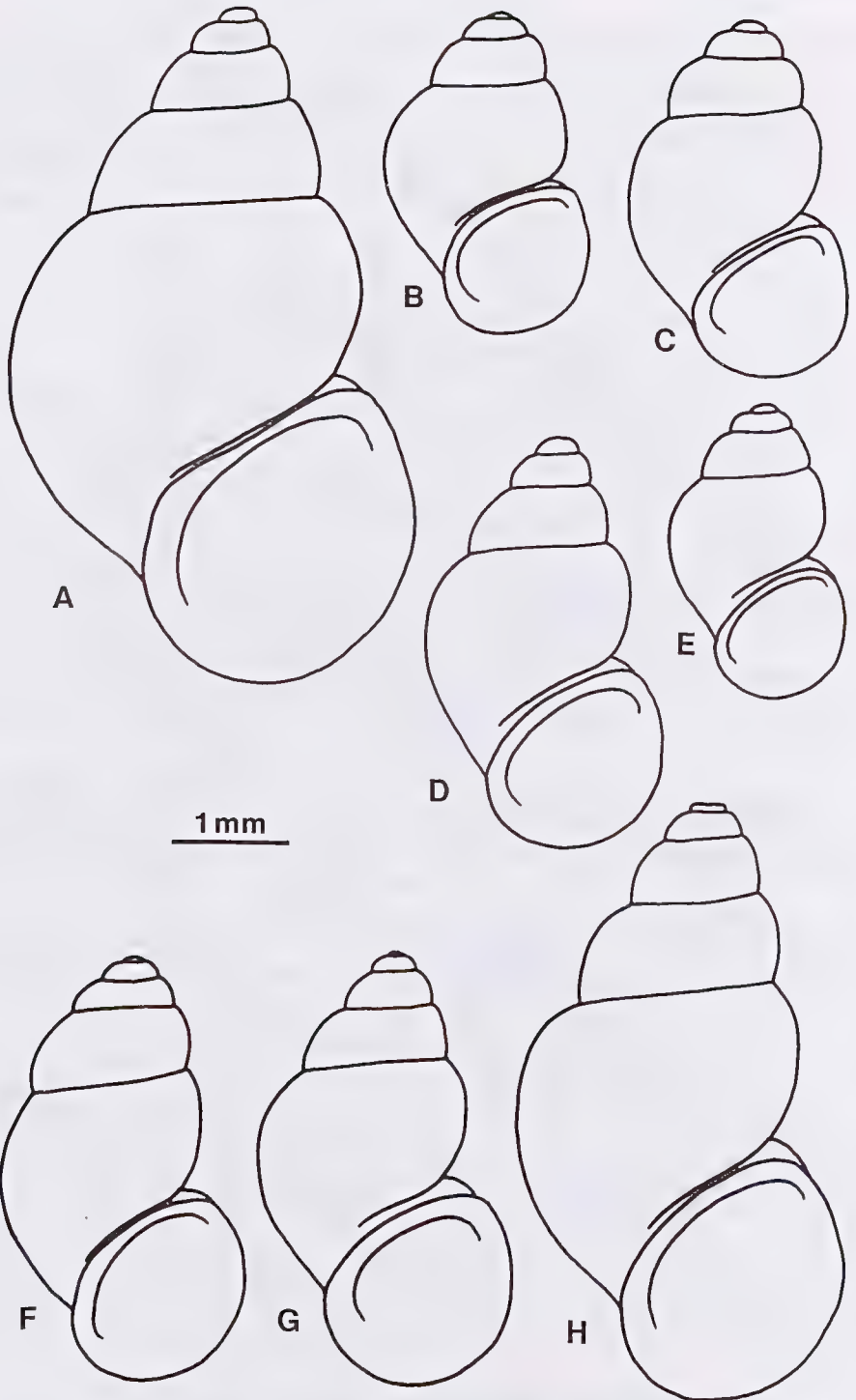


Figure 5. Shells of *Dalhousia harrisi*. A, B. Spring Ca3 (station D76), C. Spring A1 (station D4A), D. Spring E2 (station D7), E, G, H. Spring B2 (station D74), F. Spring H3 (station D19).

cd) very long, straight. Sperm sac globular, 0.34–0.46 mm in maximum length, 0.17–0.39 mm in maximum width. Albumen gland (Fig. 14A) 0.96–1.23 mm in length, 1/10–1/7 of length in pallial roof; slightly shorter than capsule gland. Capsule gland rounded anteriorly, oval in section, 1.16–1.39 mm in length, with indistinct glandular zones. Ventral channel narrow, lacking distinct vestibule, small, short opening slightly behind anterior end of capsule gland.

Distribution (Fig. 15). Common in main pool and outflow of Spring Ca1. Springs confirmed as containing this species are listed in Table 7 (Appendix 3) and include only members of the A, B, Ca, Cb, Cc, and Cd groups.

This species mostly lives in large warm pools or warm outflows from large springs ranging from 33–42°C (the majority 35–40°C).

Remarks. Data from allozyme electrophoresis presented below show, when using the criterion of sympatry, that there is no justification for recognising more than two species-group taxa within *Dalhousia*. Both are very variable in shell morphology, although *D. globosa* is generally larger and wider than the species described below. There are no known anatomical characters that can be consistently used to separate these two taxa. The allozyme differences summarized in the diagnosis are detailed below. Because of the difficulty in species-level determination and somewhat hazy species boundaries, we have selected specimens for the type series of the two species of *Dalhousia* named here from one of a few populations in which they are known to be sympatric.

There is a considerable range of variation in shell size and shape (Fig. 3. 16A,C; and Ponder, 1989, figs 11.1F, 11.2B,C,G) within this species, even within the same spring (Fig. 3A,B, 16C) or the same sample (Fig 3C,D). Mean shell length, in the seven measured populations, ranges from 2.5 to 4.27 mm (Appendix 2, Table 2) with considerable variance in some samples (Appendix 2, Table 2; Fig. 16A,C), and many populations differ significantly ($P < 0.001$) from conspecific populations in length and other dimensions and ratios. Overall there is a difference between sexes in most shell dimensions and ratios ($P < 0.1$). Allozyme variation within this taxon is detailed below (see also Appendix 3, Table 7).

Dalhousia harrisi n. sp.

Figs 2A–C, F,G, 4, 5, 7C–E, 8A,B, 9B–D, 10A,E, 11A, 12B, 13B–D, 14B,D, 15, 16B,D, 17, 22–24.

Ponder, 1989, figs 11.1A–E,G, 11.2A,D,E.

Etymology. Named for Colin Harris, as a small recognition of his efforts in the conservation of the mound springs of South Australia.

Type locality. Ca1, the main spring (Earwanyera Spring), Dalhousie Springs, South Australia.

Collection details of type material. Stn Ca1 We, Spring Ca1, 26°24'29"S 135°31'08"E, fringe of roots on steep edge at water surface on side of main pool. 12/6/1985, Coll. W. Ponder & D. Winn.

Holotype, SAM, 18939, paratypes, SAM 18940, AMS, C201744.

Diagnosis. Typically with small to medium, conical to ovate-conic shell. Distinguished electrophoretically from *D. globosa* in having high frequencies of LAP 3, SDH-1 2, SDH-2 1 and PGM-1 4 allozymes.

Description. Shell (Figs 2A–C,F,G, 4, 5). Shell opaque, small (length 2.3–3.8 mm, mean 2.8 mm, 3.1 in type series), ovate-conic to conic, SW/SL 0.64–0.80 (mean 0.71), AL/SL 0.47–0.57 (mean 0.51). Suture impressed, whorls convex to very slightly shouldered. Protoconch of about 1.5–1.6 whorls, minutely punctate. Teleoconch of 2.6–3.6 (mean 3.1) convex whorls, sutures impressed; sculpture of indistinct growth lines only. Aperture slightly longer than wide, AW/AL 0.87–1.01 (mean 0.94, 0.91 in type series) and angled posteriorly. Peristome entire, with sharp edge, weakly thickened internally, with inner lip attached to, or slightly separated from, parietal wall. Colour

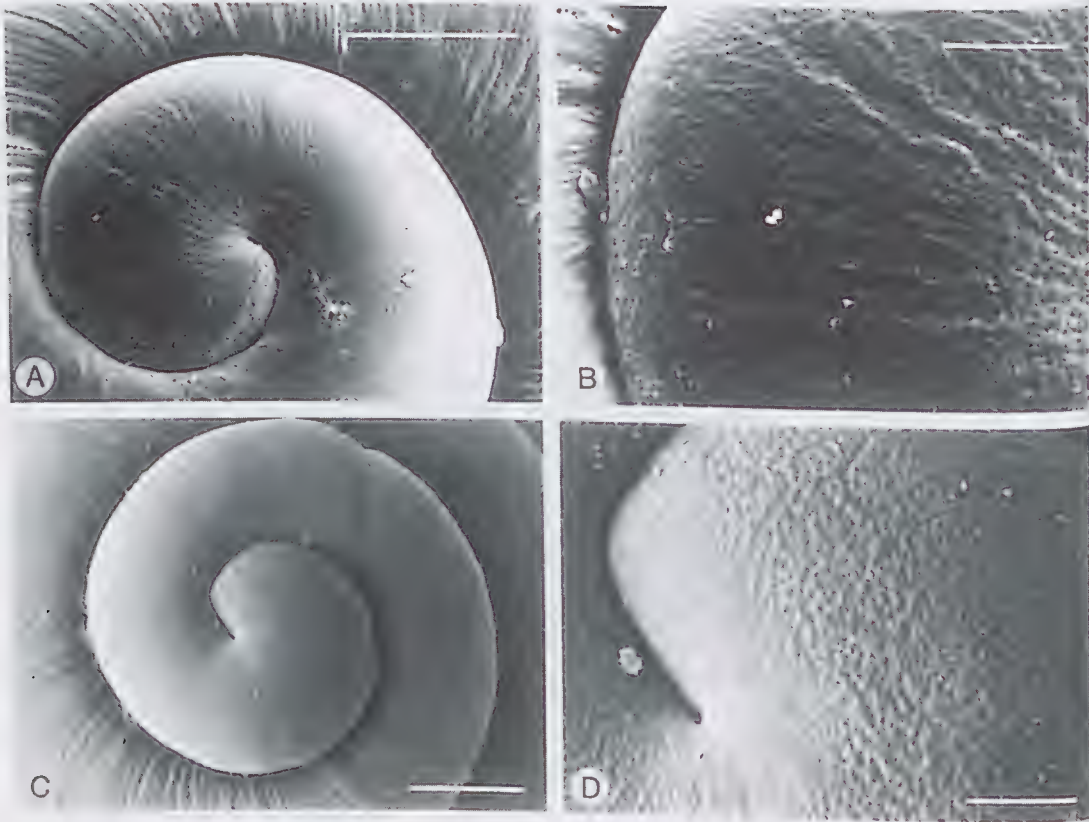


Figure 6. Protoconchs of *Dalhousia* species and *Fluvidona centralia*. A,B. *Dalhousia globosa*, Spring Ca1. C,D. *F. centralia*, Spring E1 (station D62). Scales A,C – 0.1mm, B,D – 0.025mm.

(imparted by periostracum) yellow-brown (some populations very dark brown or orange brown depending on environment). There is no significant sexual dimorphism in shell size in the type population.

Dimensions of holotype.

	SL	SW	AL	AW	BW	TW
Holotype	3.20	2.52	1.79	1.52	2.69	2.6
Figured paratype (AMS, C.201745)	3.92	2.90	2.09	1.95	3.23	3.0
Figured specimens						
(Ca13A) (AMS, C.201746)	2.92	1.74	1.39	1.10	2.33	3.5
(Ca7) (AMS, C.201747)	2.60	1.72	1.26	1.10	2.15	3.1
	3.22	2.00	1.53	1.30	2.50	3.5



Figure 7. Opercula of *Dalhousia* species and *Fluvidona centralia*; all from inner side. A,B. *D. globosa*, Spring Ca1 (station 641c). C-E. *D. harrisi*. C, topotype (station Ca1We), D, Spring Ca13A, E, Spring Ca7 (station C644). F-H. *F. centralia*. F,G, paratypes, H, Spring E1, lower outflow (station D62). Scales 0.2mm.

Dimensions of specimens from paratype series

Females, N=11

	SL	SW	AL	AW	BW	CV	TW
Minimum	2.68	1.86	1.35	1.29	2.19	0.12	2.6
Maximum	3.70	2.60	1.88	1.64	3.01	0.19	3.6
Mean	3.16	2.28	1.64	1.49	2.60	0.16	3.1
S.D.	0.27	0.19	0.13	0.10	0.21	0.02	0.27

Males, N=9

	SL	SW	AL	AW	BW	CV	TW
Minimum	2.57	1.89	1.32	1.25	2.14	0.14	2.8
Maximum	3.45	2.53	1.79	1.59	2.77	0.19	3.6
Mean	3.00	2.16	1.55	1.41	2.45	0.16	3.2
S.D.	0.30	0.22	0.17	0.11	0.22	0.02	0.20

Shell dimensions of 50 topotypes are given in Appendix 2, along with those of additional populations of this species.

Operculum (Fig. 7C-E). Ovate, pale yellow, thin, with eccentric nucleus, with 0-5 small, weak pegs on white smear on inner side.

Statistics of 20 opercula from the type series.

Females, N=11

	OL	OW	OS	PL	PH
Minimum	1.11	0.70	0.30	0.12	0.05
Maximum	1.53	1.12	0.53	0.32	0.13
Mean	1.32	0.92	0.39	0.22	0.09
S.D.	0.12	0.11	0.07	0.06	0.03

Males, N=9

	OL	OW	OS	PL	PH
Minimum	1.11	0.77	0.26	0.17	0.07
Maximum	1.38	1.05	0.55	0.27	0.14
Mean	1.24	0.88	0.36	0.22	0.10
S.D.	0.09	0.10	0.09	0.03	0.03

Radula (Fig. 10A,E). As for *D. globosa* but central teeth usually with 3 (range 3-4) cusps on either side of the median cusp.

Head-foot. Cephalic tentacles pigmented dorsally, with or without narrow unpigmented mid-dorsal stripe; snout and dorsal neck also pigmented. Ciliation (Fig. 8A,B, 9B-D, 13C) as for generic description. Foot and opercular lobes pigmented; pallial roof and visceral coil darkly pigmented, often partly mottled.

Anatomy. Osphradium unpigmented, located at posterior quarter of ctenidium, narrowly oval, 0.22-0.40 mm in length. Ctenidium with 23-25 broadly triangular filaments, apices central to towards right; maximum width 0.32-0.48 mm, posterior-most filament overlapping pericaridum (rarely abutting or 2 filaments overlapping). Rectum straight in females, weakly arched in males. Renal organ extending 1/3-1/2 length of renal gland into pallial roof; renal gland 0.51-0.72 mm in length, 0.26-0.34 mm in width. Pericardium extending 1/3 of length into pallial roof. Stomach (Fig. 11A) with style sac 0.46-0.62 mm in length, stomach proper 0.49-0.62 mm in length, caecum absent to very small (up to 0.05 mm long).

Testis of 1.8-2.0 whorls; seminal vesicle visible externally and lies between digestive gland and testis for only 0.1-0.3 whorls behind stomach, convolute over stomach. Prostate gland (Fig. 12B)

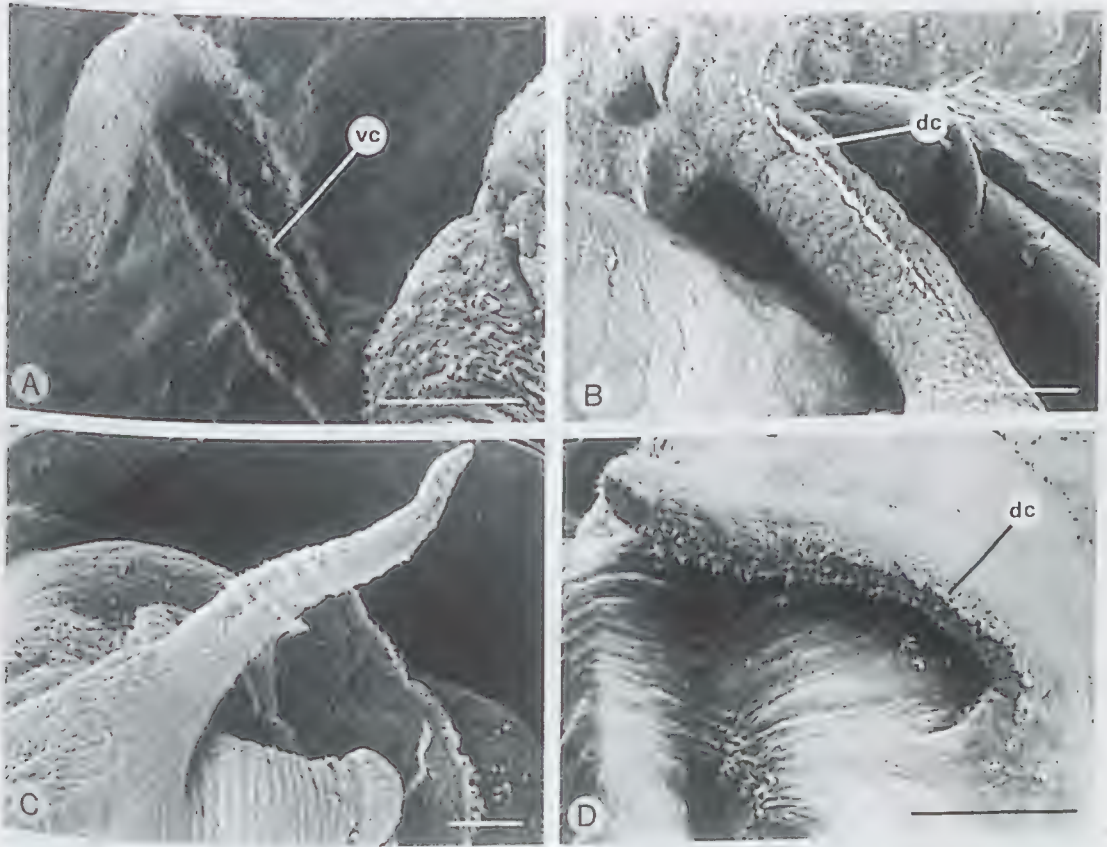


Figure 8. Cephalic tentacles of *Dalhousia* species and *Fluvidona centralia*. A,B. *D. harrisi*, Spring Ca7 (station C644). A, ventral (proximal) and laterodorsal (distal) views; B, dorsal view (also showing part of snout and foot). C. *D. globosa*, dorsal view (also showing part of snout and foot), Spring Ca1 (station 641B). D. *F. centralia*, dorsal view, Spring E1, paratype. dc - dorsal cilia; vc - ventral cilia. Scales 0.1mm.

0.42–0.43 mm in length (about 0.09–0.15 mm in pallial roof), 0.19–0.34 mm in height, broadly oval, moderately to narrowly oval in section. Pallial vas deferens undulating, unpigmented to dark grey (darker than surrounding epithelium of neck) low, rope-like ridge across neck at base of penis; a few undulations nearer prostate, straight immediately anterior to, and beneath, prostate. Penis (Fig. 13B–D) unpigmented or with proximal part of distal section of penis with grey pigmentation, basal section unpigmented or with some grey pigment; distal section long and evenly tapering, basal section relatively small, expanded. Penis base 0.35–0.38 mm from right eye, just to right of midline of head.

Ovary of 1.0–1.3 whorls. Coiled oviduct (Fig. 14B,D, co) with 1 distal U-shaped loop, orientated anteriorly to vertically; distal part arched dorsally to top of sperm sac, posteriorly, wrapped around sperm sac in S-shape coil. Duct to sperm sac anterior, very short. Common duct (Fig. 14B, cd) long, straight. Sperm sac (Fig. 14B,D, sps) globular, 0.28–0.35 mm in maximum length, 0.25–0.31 mm in maximum width. Albumen gland (Fig. 14B, ag) 0.55–0.66 mm in length, 1/7–1/4 of length in pallial roof; slightly shorter than capsule gland. Capsule gland (Fig. 14B, ag) rounded bluntly tapered anteriorly, circular to oval in section, about 0.7 mm in length, with distinct glandular zones. Ventral channel (Fig. 14B, vc) narrow, lacking distinct vestibule, small, short opening (Fig. 14B, po) at or slightly behind anterior end of capsule gland.

Distribution (Fig. 15). Found living around the water edge of the main pool of Ca1. Springs

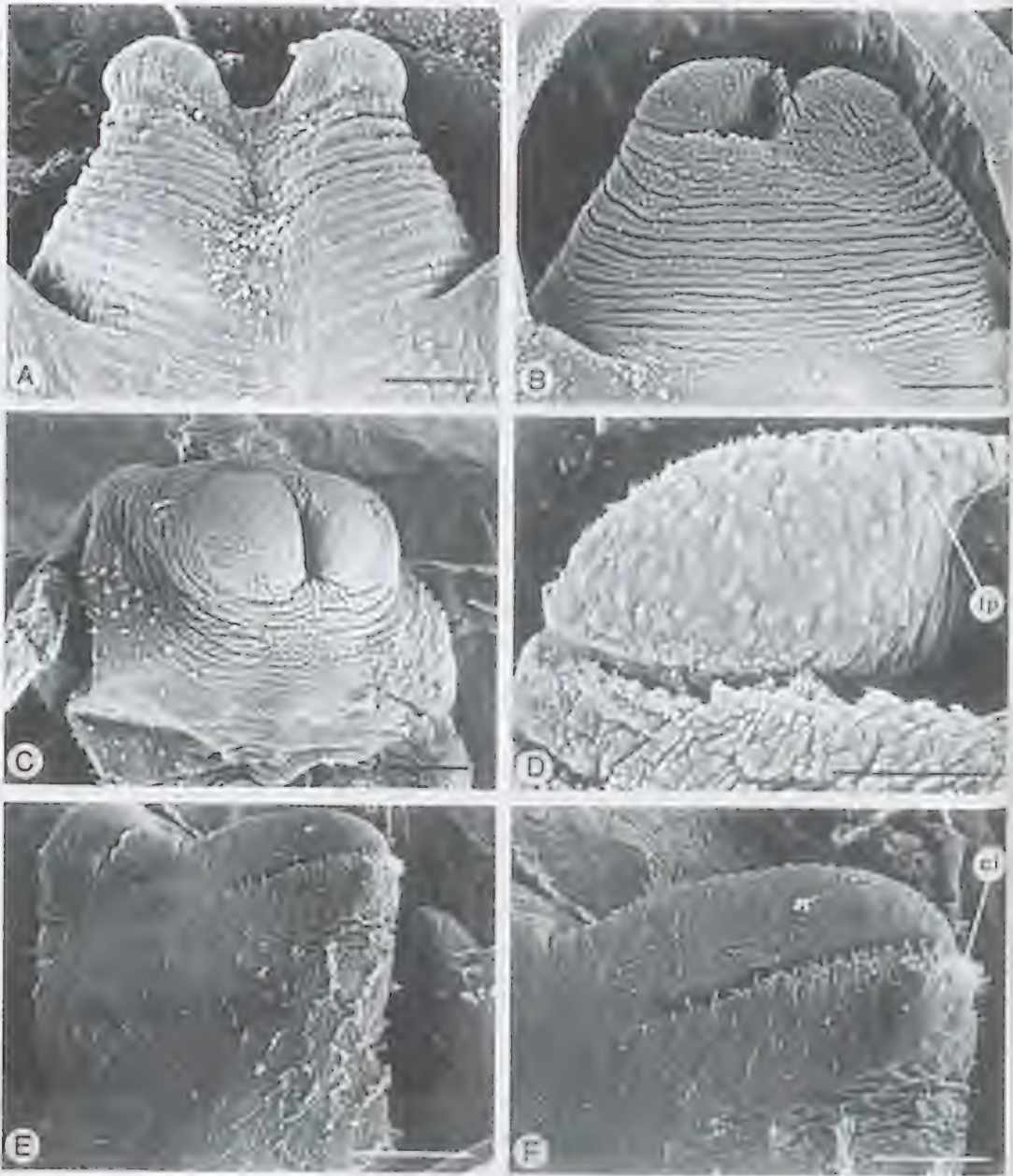


Figure 9. Snout morphology of *Dufourea* species and *Fluxidorea centralis*. A. *D. globata*, dorsal view, Spring Ca1 (station 641B). B-D. *D. harrisi*, Spring Ca7 (station C644). B,D, dorsal view, D, high power view of left labium; C, ventral view, LP. *F. centralis*, paratype. Dorsal view; F, high power view of right anterior end of snout. ci - cilia, lp - labial papillae. Scales A-C,E - 0.1mm, D,F - 0.05mm.

confirmed as containing this species are listed in Table 8 (Appendix 3).

This species lives in a wide range of habitats ranging from small cold seeps (recorded temperatures of down to 20°C), to large warm pools to very hot (up to 43°C) springs. It is found in all spring groups except the Gb subgroup.

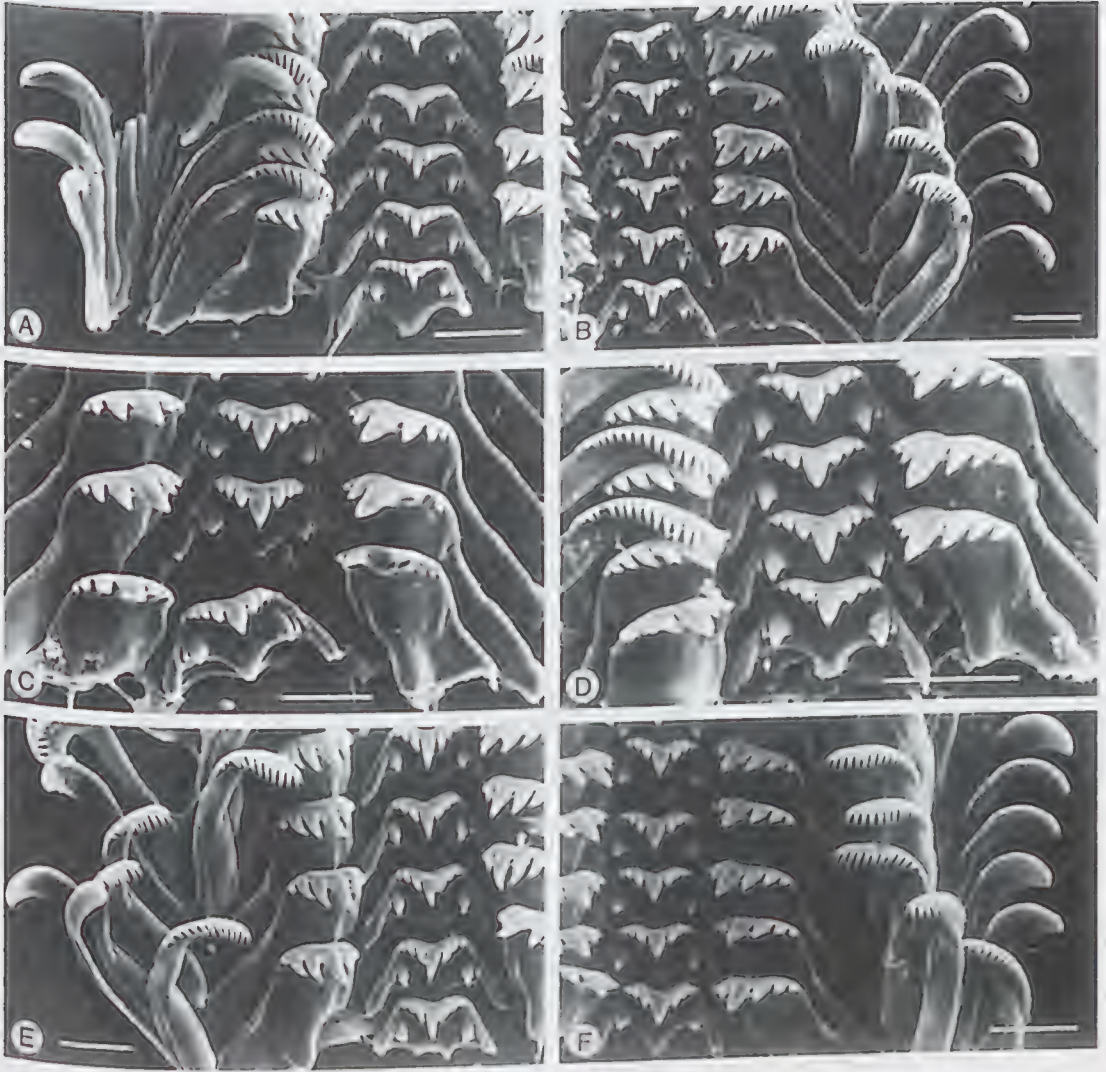


Figure 10. Radulae of *Dalhousia* species. A,E. *Dalhousia harrisi*. A, Spring Ca13A, E, Spring Ca7 (station C644). B-D,F. *D. globosa*, Spring Ca1 [station 641 (B,C) and Ca1We (D,F)]. Scales 0.02mm.

Remarks. This species is distinguishable from *D. globosa*, when in sympatry, by its generally smaller size (Fig. 16D, 22A) and taller spire. It lives in sympatry with *D. globosa* in springs Ca1, A1, A2, A8, B1, Ca8, Cc1, Cc3, and Cd1. Hybrids have been found in Ca8 and Cd2 (Appendix 3, Table 8). In Ca1 it has been found only on the edges of the large pool where it is effectively out of reach of the catfish which are known to eat hydrobiid snails (Ponder, 1989). Other than the shell characters, there are no obvious, consistent morphological synapomorphies which separate this species from *D. globosa*, although in the type population the anteriorly placed bursal duct is a consistent difference. The distribution of this character was checked in all other populations and was found to be ventrally to posteriorly placed, as in *D. globosa*. The capsule gland has more distinct glandular zones in *D. harrisi* than in *D. globosa* in most populations, but, again, this is not consistent. The genetic differences between these two taxa are summarized in the diagnosis and detailed below. Allozyme variation within this taxon is also detailed below (see also Appendix 3, Table 8).

D. harrisi is generally rather uniform in size in the northern spring groups (A and B) (Figs 16B, 16D), but varies considerably in the other spring groups (C–H) (Fig. 17). However, generally there is a considerable amount of variation in shell size and shape within this species (Appendix 2, Table 2; Figs 4, 5, 17; Ponder, 1989, figs 11.1A–E,G, 11.2A,D,E). The type population (Fig. 2A,B) is more similar to *D. globosa* in shell shape than most others (compare Figs 2A,B with 2H), although rather globose specimens are encountered in other populations (e.g. Fig. 4A,B,D). Mean shell size, in the 36 measured populations, ranges from 1.5 to 4.1 mm (Appendix 2, Table 2) with considerable variance in some populations (Table 2, Fig. 17, and compare Figs 4A,B, D; 4C,E; 4F,G; 4H,I; 5A,B; 5E,G,H), and many populations differ significantly ($P < 0.001$) from conspecific populations in length and other dimensions and ratios. Overall there is a significant ($P < 0.001$) difference in most shell dimensions and ratios between sexes. Comparisons with *D. globosa* show a significant ($P < 0.001$) difference in all measured shell dimensions and their ratios.

Several populations of *D. harrisi* have a proportion of individuals infected with parasites. In some samples the infected individuals are significantly larger than other members of the population but in others this is not the case. Eliminating parasitized individuals does not markedly alter the patterns of variation in shell size.

Genus *Fluvidona* Iredale, 1937

Type species: *Hydrobia petterdi* Smith, 1882.

Remarks. The anatomy of the Wilson's Promontory species of this genus is described in detail by Ponder *et al.* (1994). The species described below is included in *Fluvidona* because its radular, anatomical, opercular and shell characters agree with members of that genus in most respects. There are only two significant anatomical differences between this taxon and other species of *Fluvidona*. One is the position of the bursal duct which is located at the ventral end of the anterior edge of the bursa copulatrix in most individuals, whereas it opens in the middle of the anterior edge in other species of *Fluvidona*. The second character is the long, tapering penis with a narrow (not wide) base which is not markedly set off from the distal part of the penis as in other members of the genus.

The genus name *Fluvidona* is used following Ponder *et al.* (1994) but electrophoretic studies by one of us (S.A.C., in prep.) indicate that typical *Fluvidona* from northern NSW is generically distinct from the southern species attributed to this genus.

Fluvidona centralia n. sp.

Figs 2D,E, 6C,D, 7F–H, 8D, 9E,F, 12D, 18–19–20–21, 25.

Etymology. *Centralia* – refers to the centre of Australia.

Type locality. Spring Cd11, Dalhousie Springs, South Australia.

Collection details of type material. Stn. D70, Spring Cd11, 26°24'40"S 135°30'29"E, small seepage on large mound, temp. 24°C, 9/5/1990, Coll. DC SC.

Holotype, SAM, 18941; paratypes, SAM, 18942; AMS, C.201748.

Diagnosis. With small, conical shell, prominent opercular pegs, 4–5 pairs of basal cusps on central teeth of radula, a ventrally located bursal duct and a narrowly tapering penis with a long, narrow base.

Description. Shell (Fig. 2D,E, 18). Shell opaque, small (1.4–2.2 mm, mean 1.8 mm), conical, SW/SL 0.56–0.67 (mean 0.62), AL/SL 0.36–0.46 (mean 0.40). Protoconch (Fig. 6C,D) of about 1.25 whorls, distinctly punctate. Teleoconch of 2.7–3.5 (mean 3.1) convex whorls, sutures moderately

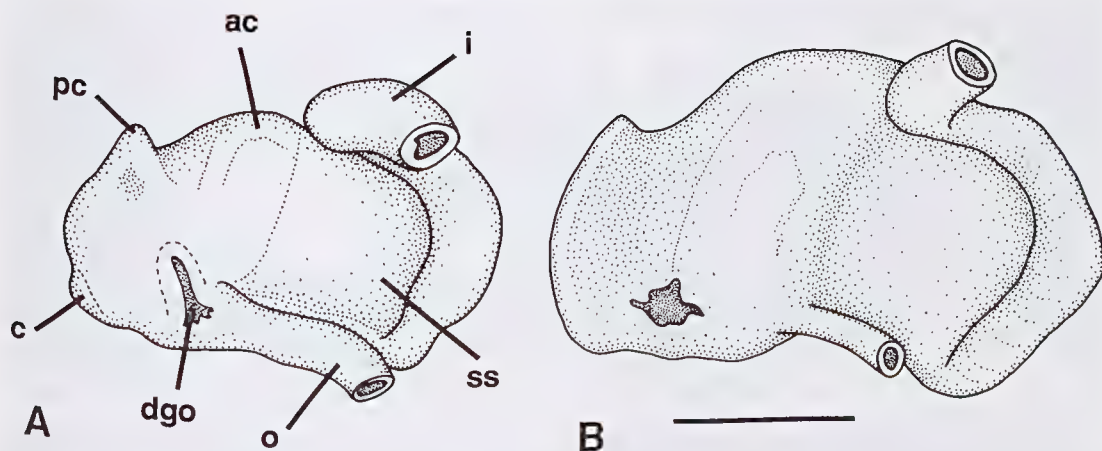


Figure 11. Stomachs of paratypes of *Dalhousia* species, viewed from the left side. A: *D. harrisi*. B: *D. globosa*. ac – anterior gastric chamber, c – caecum, dgo – digestive gland opening, i – intestine, o – oesophagus, pc – posterior gastric chamber, ss – style sac. Scale 0.5mm.

impressed; sculpture of indistinct growth lines only. Aperture usually slightly longer than wide, AW/AL 0.75–1.06 (mean 0.94), angled posteriorly. Peristome slightly thickened internally, entire, with thin inner lip attached to parietal wall; external varix absent. Colour yellow-brown to brown due to periostracum. There is no significant sexual dimorphism in shell size in the type population.

Dimensions of holotype.

	SL	SW	AL	AW	BW	TW
Holotype	2.02	1.21	0.86	0.76	1.39	3.0
Figured specimen, D62 (AMS, C.201749)	2.77	2.26	1.12	1.03	2.05	3.6

Dimensions of specimens from paratype series

Female, N=5

	SL	SW	AL	AW	BW	CV	TW
Minimum	1.72	1.03	0.69	0.68	1.29	0.11	2.7
Maximum	2.17	1.27	0.86	0.81	1.58	0.20	3.3
Mean	1.89	1.18	0.79	0.74	1.43	0.16	3.05
S.D.	0.18	0.10	0.07	0.05	0.11	0.04	0.20

Male, N=15

	SL	SW	AL	AW	BW	CV	TW
Minimum	1.47	0.89	0.60	0.55	1.07	0.10	2.7
Maximum	2.14	1.28	0.79	0.77	1.46	0.22	3.5
Mean	1.79	1.10	0.71	0.66	1.30	0.16	3.09
S.D.	0.20	0.11	0.07	0.06	0.11	0.03	0.22

A summary of the shell measurements of additional populations of this species are given in Appendix 2, Table 3.

Operculum (Fig. 7F–H). Ovate, thin, pale yellow, with eccentric nucleus, with 1–4 well-developed pegs emerging from white smear on inner side.

Statistics of 20 opercula from the type series.

Female, N=5

	OL	OS	PL	PH	PN
Minimum	0.67	0.11	0.08	0.04	2
Maximum	0.82	0.24	0.16	0.11	4
Mean	0.76	0.18	0.11	0.07	3
S.D.	0.06	0.05	0.03	0.03	0.71

Male, N=15

	OL	OS	PL	PH	PN
Minimum	0.62	0.11	0.04	0.03	1
Maximum	0.82	0.25	0.19	0.18	4
Mean	0.71	0.17	0.10	0.09	2.93
S.D.	0.06	0.04	0.04	0.05	0.96

Radula (Fig. 19). Central teeth broad, each with 4-6 (usually 5) small, triangular cusps on either side of a sharp median cusp about twice the length of the adjacent cusps. 3-4 pairs of lateral basal denticles present, innermost larger. Lateral teeth with largest cusps in tooth row, 4-5 on inner side of

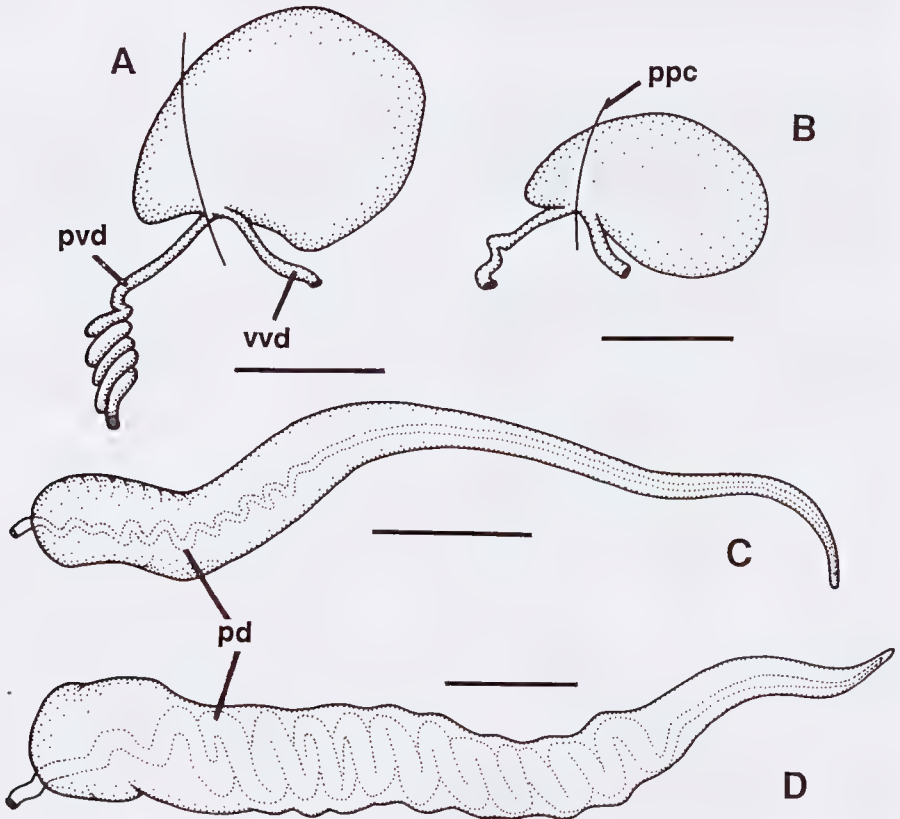


Figure 12. Male genitalia of paratypes of *Dalhousia* species and *Fluideona centralia*. A. Prostate gland of *Dalhousia globosa* viewed from left side. B. Prostate gland of *Dalhousia harrisi* viewed from left side. C. Penis of *Dalhousia globosa*. D. Penis of *Fluideona centralia*. pd - penial duct, ppc - posterior end of pallial cavity, pvd - pallial vas deferens, vvd - visceral vas deferens. Scales A, B - 0.25mm, C - 0.5mm, D - 0.1mm.

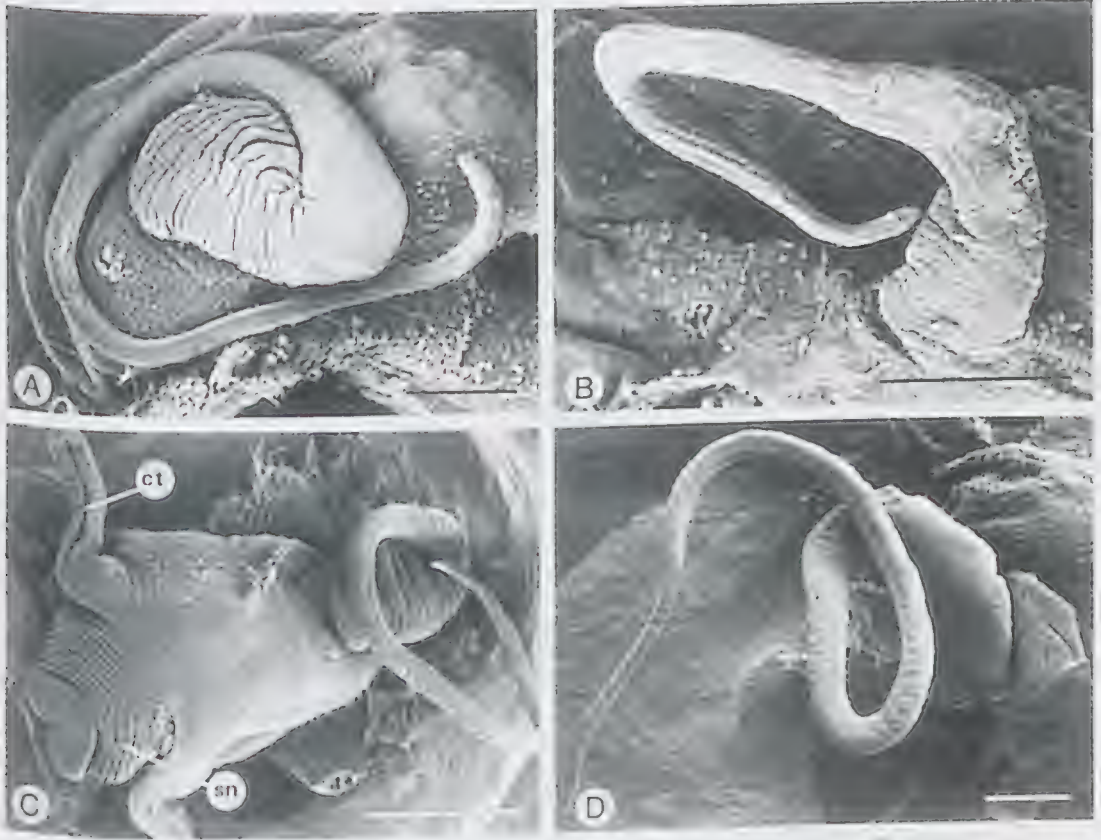


Figure 13. Head and penes of *Dalhousia* species. A. penis of *D. globosa*, Spring Ca1 (station C641B). B, D. Penes of *D. harrisi*, B, Spring Ca7 (station C644); D, Spring Ca1 (station C641A). C. Head and penis of *D. harrisi*, Spring Ca1 (station C641A). ct - cephalic tentacle; sn - snout. Scales A,B,D - 0.2mm, C - 0.5mm.

large triangular median cusp and 4-6 (usually 5 or 6) on outer side. Inner marginal teeth with 25-27 narrow, sharp cusps on antero-distal and outer-distal edge. Outer marginal teeth with 27-33 small, narrow, sharp cusps (approx. half length of those on inner marginal teeth) on antero-distal and inner-distal edge. (Description based on 4 radulae).

Head-foot. Animal unpigmented except for pigment patches on head behind eyes and mid-dorsally; opercular lobe usually unpigmented, rarely with trace of pigment. Ciliation on snout (Fig. 9E,F) well developed laterally, a narrow, but well-developed band laterally and latero-dorsally just behind labia, and scattered cilia dorsally. Cephalic tentacles with well-developed dorsal band of cilia (Fig. 8D) which extends most of length of tentacle, and a pair of weaker ventro-lateral bands.

Anatomy. Osphradium unpigmented, located just behind middle of ctenidium. Ctenidium with 14-16 broadly triangular filaments, apices near right side (0.06-0.15 mm from left side, maximum width 0.12-0.17 mm; abuting (or one filament overlapping) pericardium. Rectum with small to moderate U-shaped bend. Renal organ extending 1/3 to 1/2 of length into pallial roof; renal gland 0.31-0.39 mm in length, 0.17-0.20 mm in width. Pericardium extending about 1/2 of length into pallial roof. Stomach (Fig. 20D) with style sac 0.32-0.43 mm in length, stomach proper 0.39-0.46 mm in length. Gastric caecum small to minute (0.01-0.20 mm in length).

Testis of 1.0-1.2 whorls; seminal vesicle beneath half whorl of testis behind stomach, moderately to markedly convolute over stomach. Prostate gland 0.31-0.32 mm in length (about half in pallial

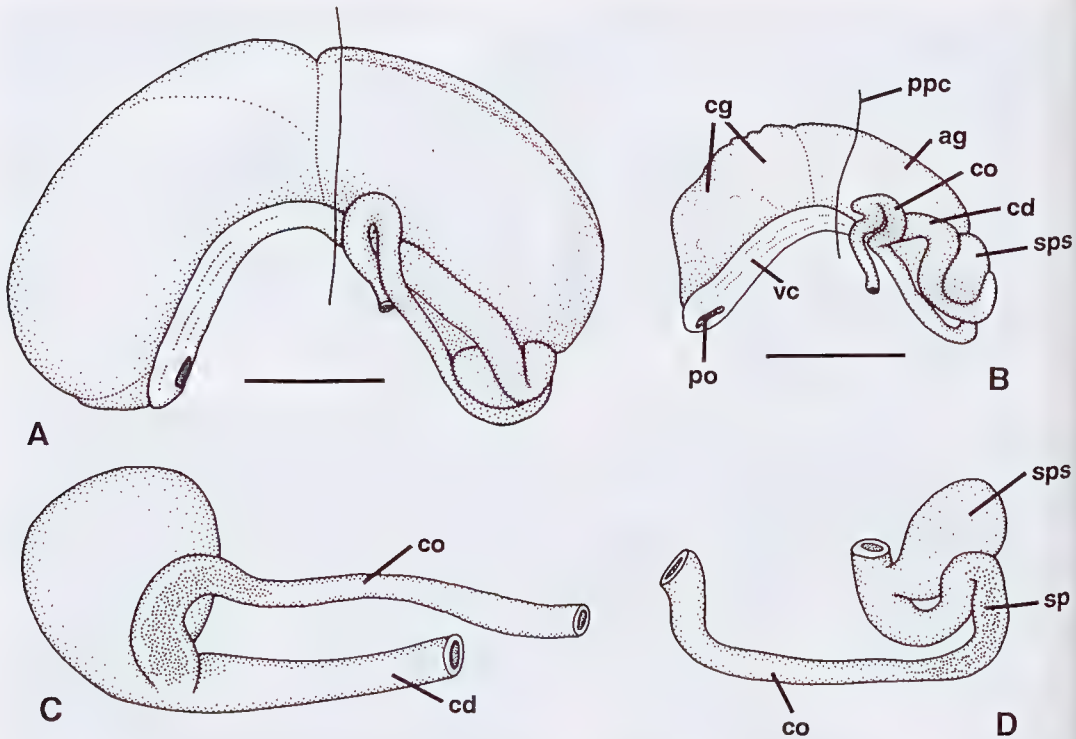


Figure 14. Female reproductive systems of paratypes of *Dalhousia* species. A,C. *D. globosa*. A, oviduct viewed from left side; C, detail of sperm sac and associated oviduct. B,D. *D. harrisi*. B, oviduct viewed from left side; D, detail of sperm sac and associated oviduct. ag - albumen gland, cd - common duct, cg - capsule gland, co - coiled oviduct, po - pallial opening of oviduct, ppc - posterior pallial wall, sp - sperm stored in oviduct, sps - sperm sac, vc - ventral channel. Scales (A,B) 0.5mm.

roof), bean-shaped, oval to narrowly-oval in section. Pallial vas deferens emerges ventrally from posterior end of pallial portion of prostate gland, straight until near penis where it weakly undulates. Penis (Fig. 12D) unpigmented, distal part short, narrow, tapering, tapers gradually into long, narrow, slightly tapering base. Penial duct strongly undulating in base, straight in distal section. Penis located just to right of midline, 0.19–0.25 mm behind right eye.

Ovary of 0.6–0.9 whorls. Coiled oviduct (Fig. 20A,B, co) with double loop, anterior U-shape bent anteriorly and posterior loop, details variable (c.f. Fig. 20A and B); distal part with weak elbow just before opening ventrally to bursal duct well behind posterior pallial wall (Fig. 20C). Common duct (Fig. 20C, cd) straight to pallial wall. Seminal receptacle (Fig. 20C, sr) ovoid, 0.08–0.12 mm in length, 0.01–0.08 mm in width, at anterior edge of bursa; duct short. Bursa copulatrix (Fig. 20A–C, bc) ovoid to elongate-ovoid, (0.14–)0.29 mm in maximum length and width; bursal duct simple, 0.06–0.08 mm long, emerging from antero-ventral face (more nearly mid anterior in one specimen). Albumen gland (Fig. 20A,B, ag) 0.19–0.31 mm in length, 1/6–1/4 of length in pallial roof; length relative to capsule gland variable (0.5 to 1.12) (c.f. Figs 20A and B). Capsule gland (Fig. 20A,B, cg) truncated anteriorly, 0.26–0.37 mm in length, oval to narrowly oval in section. Ventral channel (Fig. 20A,B, vc) broad, lacking distinct vestibule, short, slit-like opening (Fig. 20A,B, po) beneath anterior end of capsule gland.

Distribution (Fig. 15). Springs known to contain this species are listed in Table 9 (Appendix 3).

This species lives in a few small (mainly cold) seeps, and in the shallow, lower outflow of at least

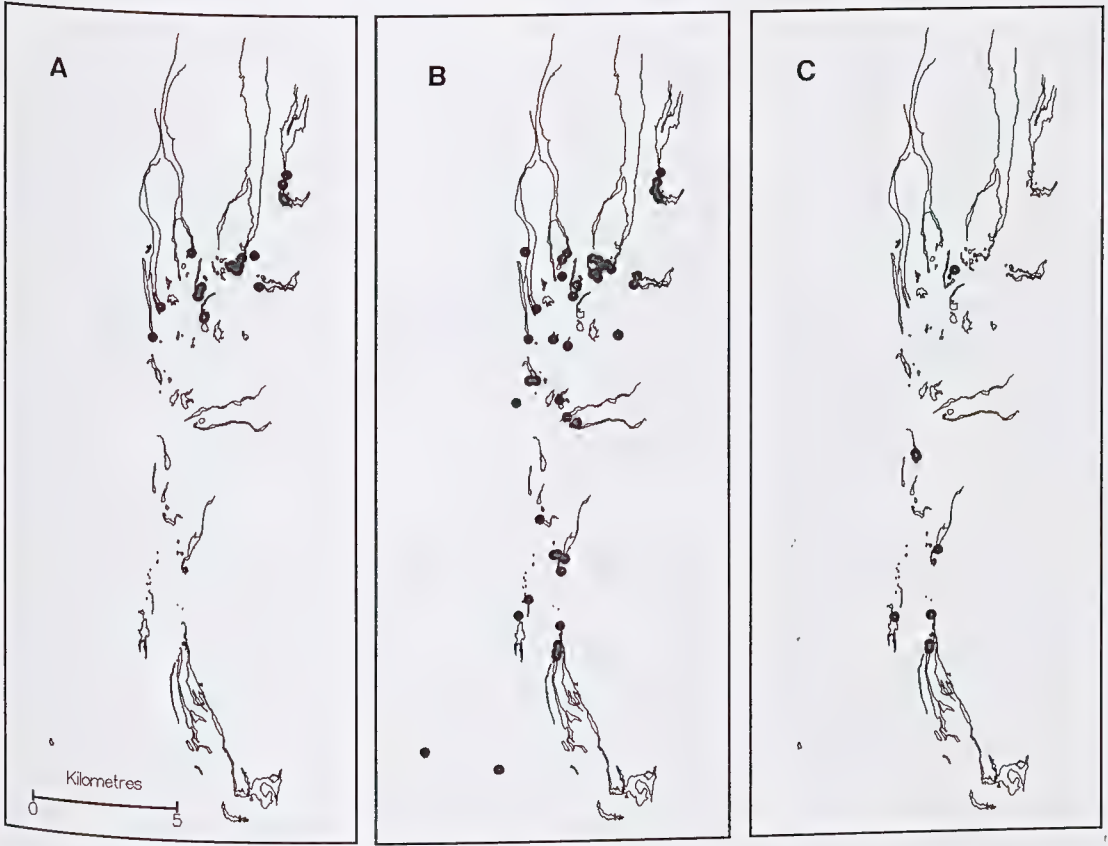


Figure 15. Distribution of *Dalhousia* species and *Fluvidona centralia*. A. *D. globosa*. B. *D. harrisi*. C. *F. centralia*.

one of the large springs. It has not been found living in sympatry with *Dalhousia*.

Remarks. This species is readily distinguished from the somewhat similar forms of *D. harrisi* with small, conical shells in having a more evenly conical spire outline. In addition, *F. centralia* differs from both species of *Dalhousia* in having more prominent opercular pegs, multiple (not two) basal denticles on the central teeth and there are considerable differences in the female genital system (compare Figs 14 and 20) and penial morphology (compare Fig. 12C,D).

Apart from the type population, a sample from a lower, cold outflow from a large spring (E1, stn. D62) was also examined in detail but proved (unlike the type population) to be heavily parasitised. The external features of the animal show the same ciliation patterns but the opercula differ in having more numerous pegs (2–7, mean 4.2) than the Cd11 sample. Radulae also differed, having fewer cusps (4–5, usually 4 on each side of median cusp on central teeth; 4 on inner side of lateral teeth and 4–5 on outer side; 18–21 cusps on inner marginals and 26–32 on outer marginals). Unfortunately most of the other samples contained insufficient material for detailed analysis so the range of variation within most populations of this taxon has not been adequately ascertained. Given the differences between the Cd11 and E1 populations, further work may well show that subdivision of this taxon is possible and this is also suggested by the level of genetic variation within the taxon (described below). In addition, given the nature of the localities frequented by this taxon, it is undoubtedly under represented in our sampling. The small seepages are often difficult to locate due to the dense vegetation and can be very easily missed. In addition, sampling the cold outflows of the

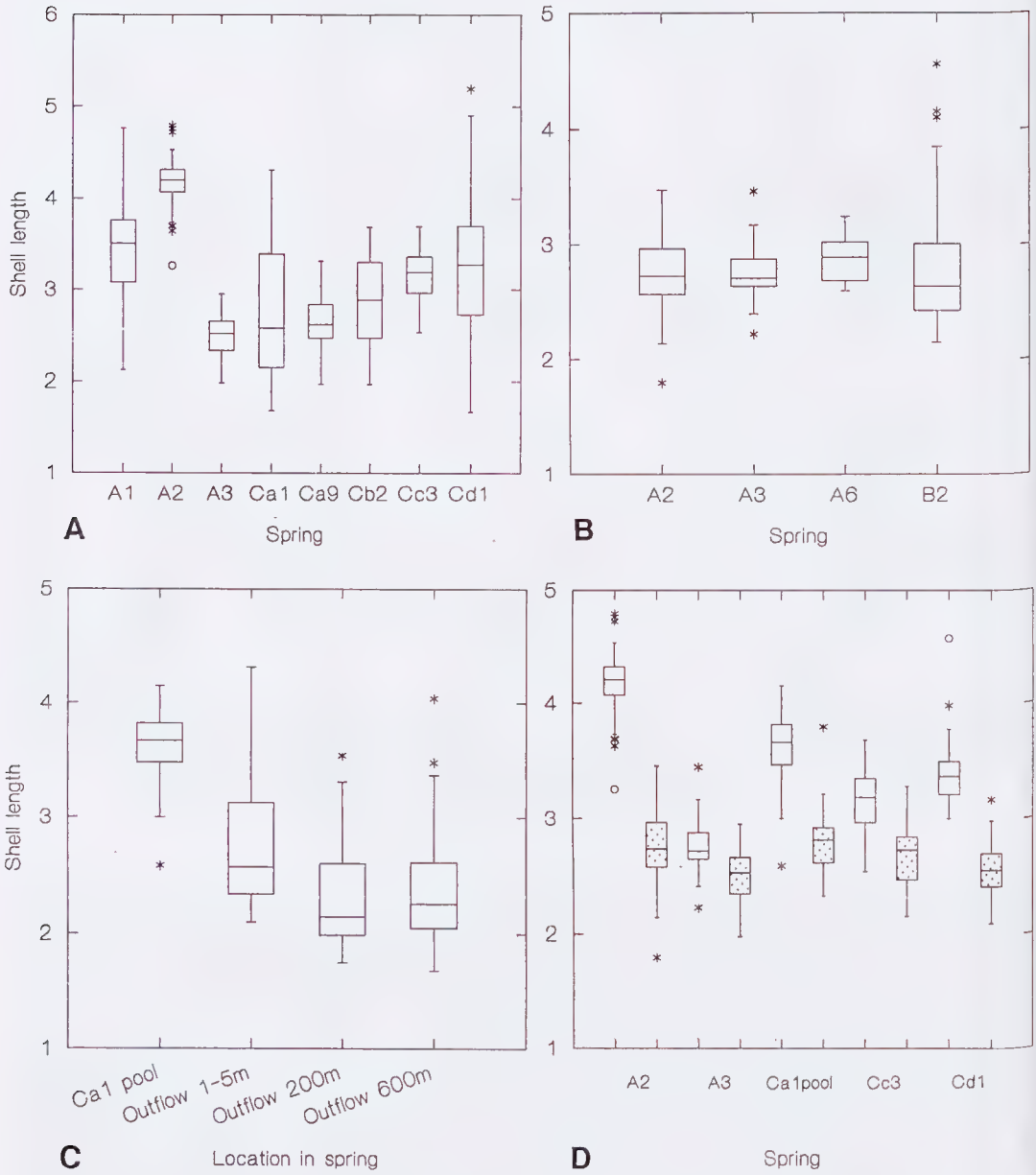


Figure 16. Box plots showing variation in shell length in *Dalhousia globosa* and *D. harrisi*. A. Shell lengths of *D. globosa*. Note that the data for Ca1 are pooled from the samples shown separately in C. B. *D. harrisi* showing variation in shell size in the A and B spring groups. C. *D. globosa*, showing variation in shell size in different sites in Spring Ca1. D. Comparison of shell lengths of *Dalhousia globosa* and *D. harrisi* (stippled) in some of the springs in which they are sympatric. The median (the mid-point of the ordered numbers) is marked inside the box, the ends of the boxes splitting the ordered numbers in half again. Outliers are represented by an asterisk and extreme outliers by a circle.

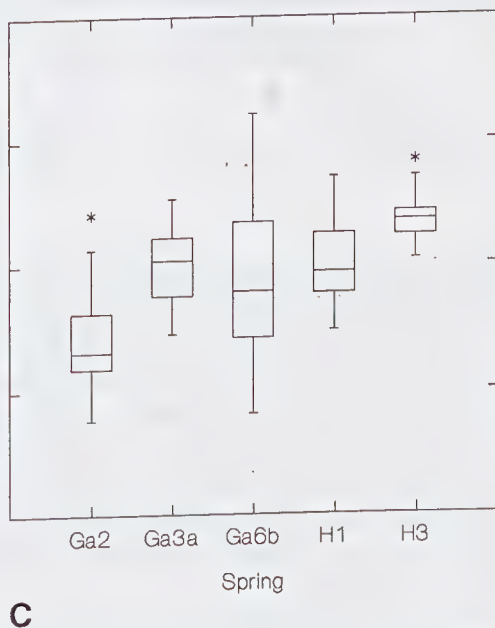
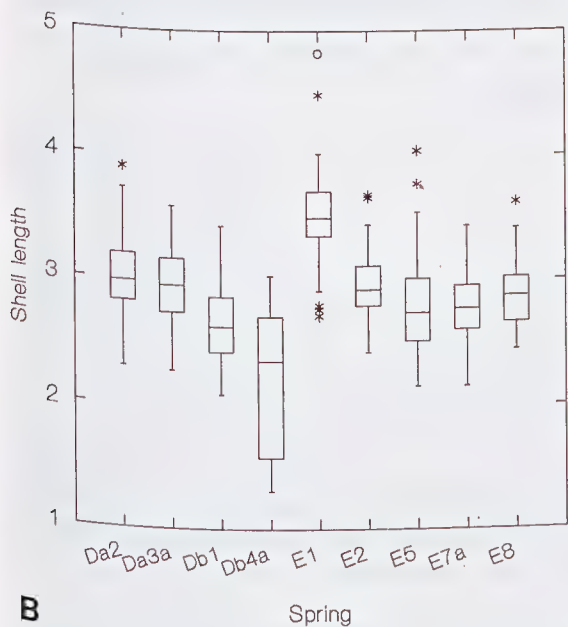
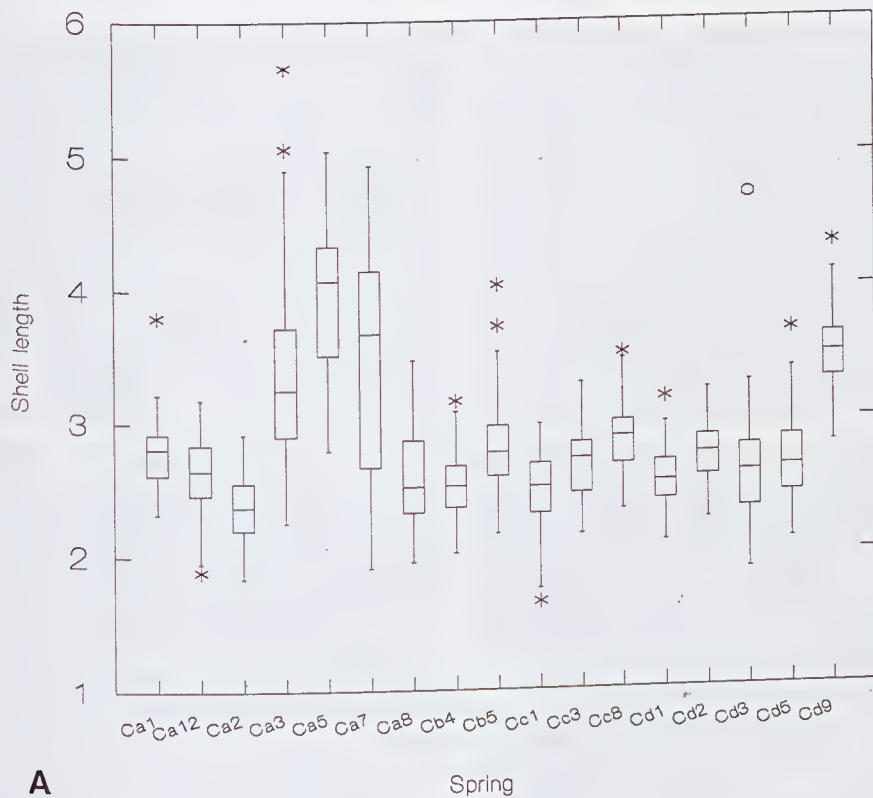


Figure 17. Box plots showing variation in shell length of *Dalhousia harrisi*. A. The C-group springs. B. The D and E-group springs. C. The G and H-group springs. For an explanation of box plots see Figure 16.

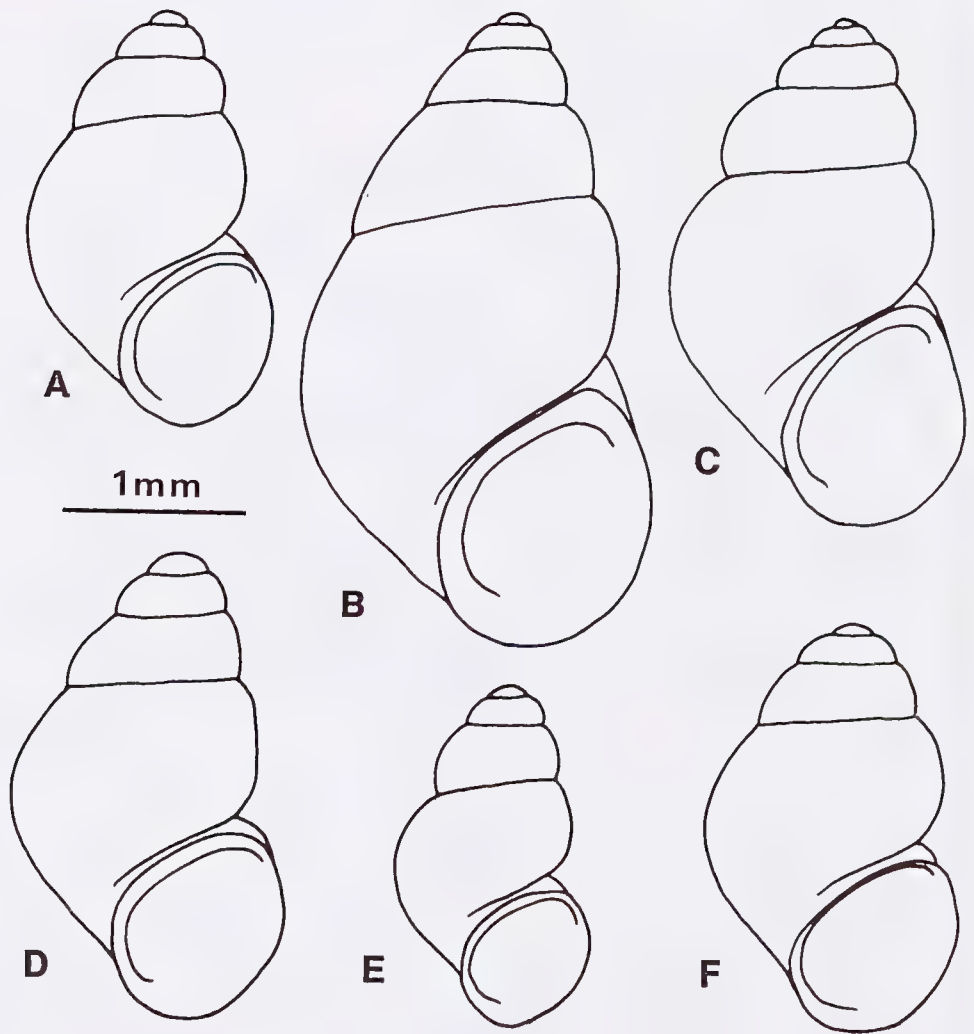


Figure 18. Shells of *Fluvidona centralia*. A. Spring Ga1 (station D13), B. Spring Ga2 (station D5), C. Spring F9 (station D53), D. Spring E3 (station D23A), E. Spring Cd11 (station D70; paratype), F. Spring Ga6A (station D15).

large springs is also difficult because of the dense vegetation and the snails, in this type of habitat, are usually very infrequent. Shell variation between populations is shown in Fig. 18.

The genus *Jardinella* (see Ponder and Clark, 1990) found in artesian springs in western Queensland, as well as in some coastal rivers in north Queensland (Ponder, 1991) is similar to *Fluvidona* in having a small seminal receptacle and large bursa copulatrix but differs in having, like *Dalhousia* and *Fonscochlea*, only two pairs of basal denticles on the central radular teeth and weak opercular pegs.

The new species represents a major range extension for *Fluvidona*, a predominantly south eastern Australian group, although undescribed taxa are known from the Flinders Ranges, as well as more coastal areas in South Australia. As noted above, the new species differs from any of the named taxa

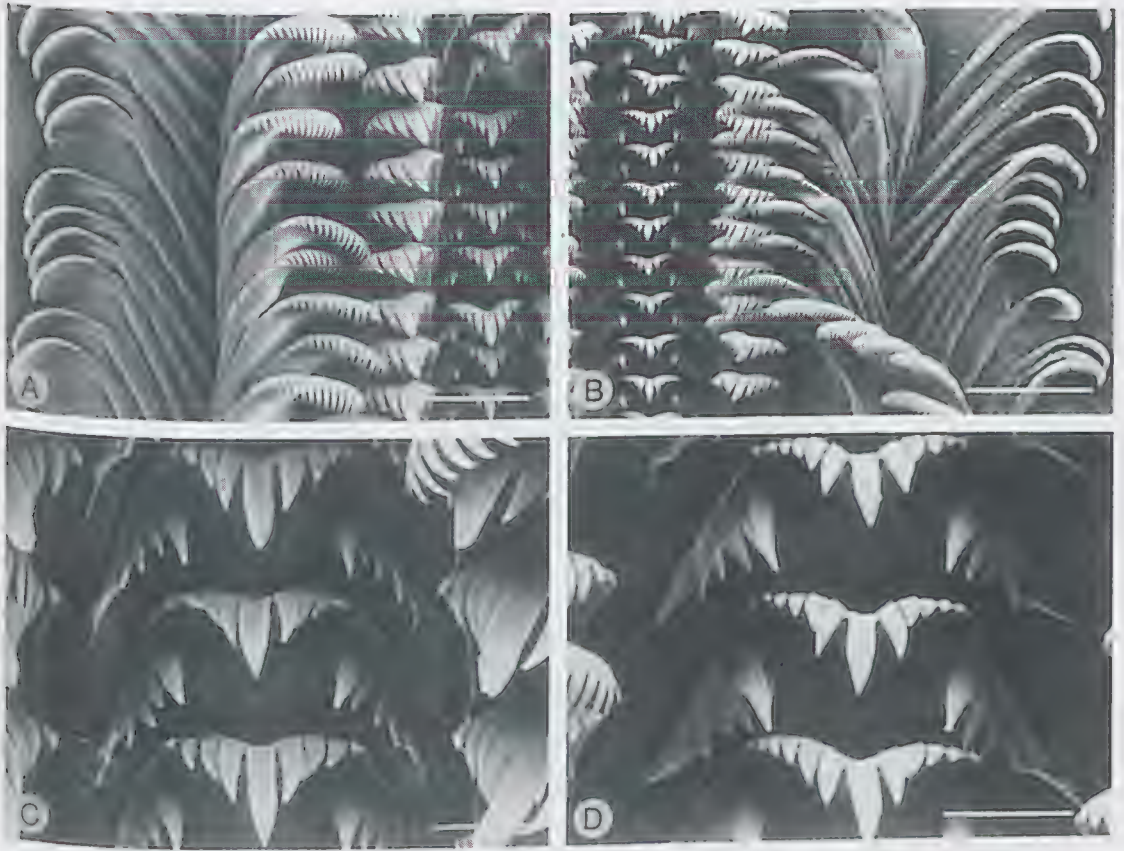


Figure 19. Radulae of *Fluvidona centralia*. A,C. Spring E1 (station D62), C, detail of central teeth. B,D. Paratype. Spring Cd11 (station D70), D, detail of central teeth. Scales A,B – 0.02mm, C,D – 0.005mm.

in having the bursal duct opening antero-ventrally to the bursa and in having a gradually tapering penis with a narrow base.

Allozyme electrophoresis.

Gene frequency tables are given for the three taxa in Appendix 3. Our results confirm that the snails are grouped into two lineages, *Dalhousia* and *Fluvidona*. *Dalhousia* is the dominant component and is widespread throughout the Dalhousie Spring system. The second group was found in only seven localities, predominantly in the small seepages and in the lower, swampy outflow from a large spring (E1). Allozyme mobilities and activities differ so much between these two groups that no evolutionary relation between them can be discerned. Consequently, the allozymes within each group were named and analysed separately.

Dalhousia can be sub-divided into at least two genetic species recognised on the basis of characteristic suites of allozymes. *D. globosa* is characterised by very high frequencies of the *Lap* 2, *Pgm*-2 3, *Sdh*-1 1 and *Sdh*-2 2 alleles, and a high frequency of the *Gpi* 2 allele. These allozymes are virtually absent or found in very low frequencies in *D. harrisi* which is characterised by high frequencies of *Lap* 3 and *Pgm*-1 4, which are virtually absent in *D. globosa*, *Sdh*-1 2 and *Sdh*-2 1. With the exception of samples from Ca8 and Cd2 springs, where there appears to be a breakdown of isolating mechanisms, there were very few heterozygotes at the *Lap* or *Pgm* loci which comprised a characteristic allele from each of *D. harrisi* and *D. globosa*. Individual snails were scored and

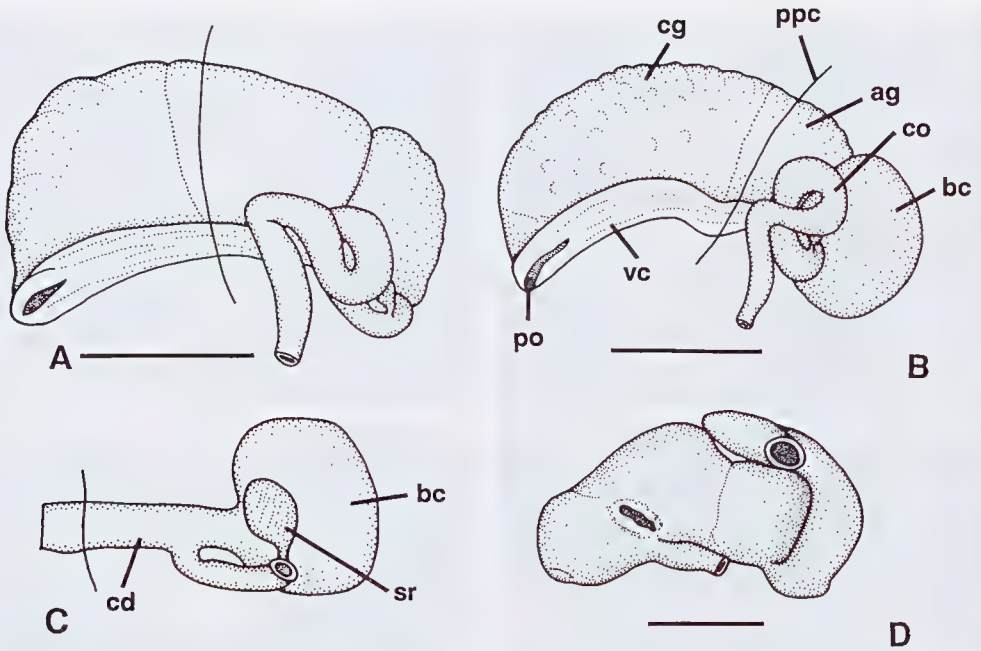


Figure 20. Female reproductive system and stomach of *Fluvidona centralia*. A,B. Oviducts of two paratypes viewed from the left side, showing variation in coiling pattern of coiled oviduct and relative length of albumen gland. C. Detail of bursa copulatrix, seminal receptacle and associated ducts from left side. D. Stomach from left side (see Figure 8 for labels). ag – albumen gland, bc – bursa copulatrix, cd – common duct, cg – capsule gland, co – coiled oviduct, po – pallial opening of oviduct, ppc – posterior pallial wall, sr – seminal receptacle, vc – ventral channel. Scales 0.25mm.

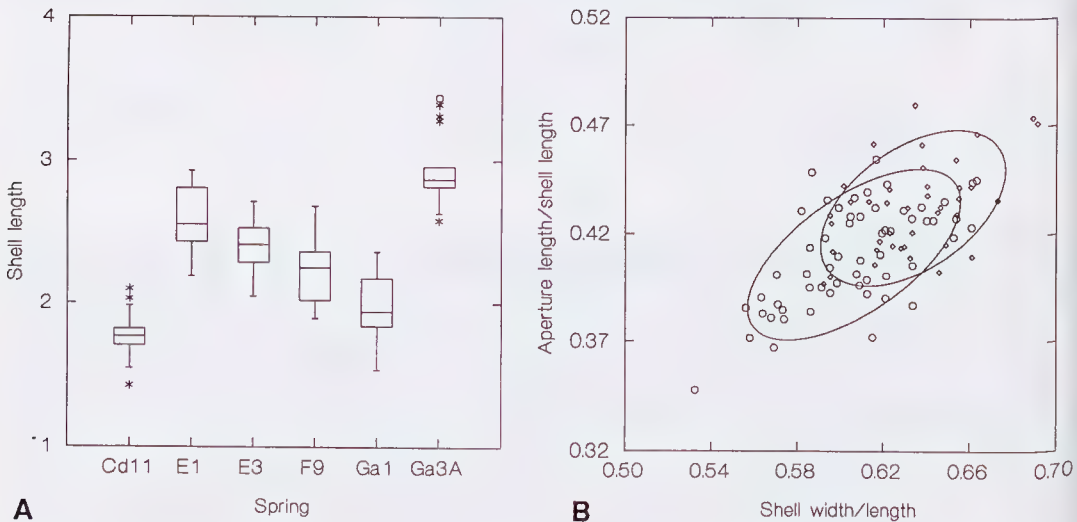


Figure 21. A. Box plots showing variation in shell length of *Fluvidona centralia* (For an explanation of box plots see Figure 16). B. Separation of the two electrophoretically distinct groups within *F. centralia* using two shell ratios. Samples from springs Cd11, E1 and F9 are represented by circles, those from springs E3 and Ga1 by diamonds. The ellipse represents 75% of the variance.

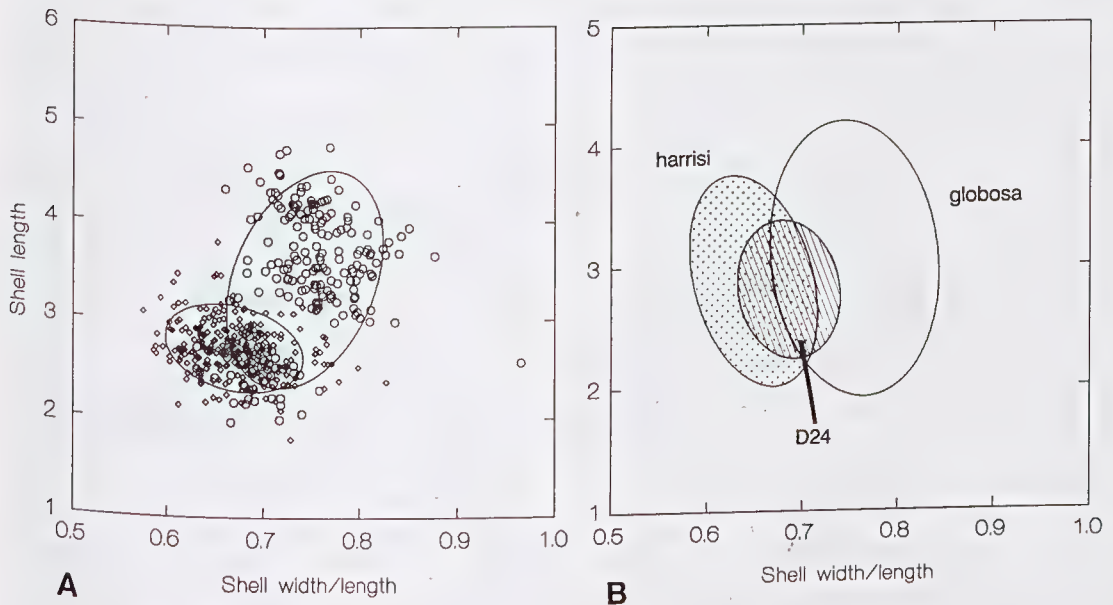


Figure 22. A. Plot of shell length and the ratio of shell width/length for sympatric populations of *Dalhousia globosa* (circles) and *D. harrisi* (diamonds). B. Plot of shell length and the ratio of shell width/length for all measured populations of *Dalhousia globosa* (except station D24), Ca1a (station D24) and *D. harrisi*. The ellipses in both figures contain 75% of the variance. The individual data points have not been plotted in B.

allocated to one of these genetic species on the basis of their allelic constitution for these loci. In springs Ca8 and Cd2, snails were allocated to *D. globosa* if they were homozygous for *Lap 2*, to *D. harrisi* if they were homozygous for *Lap 3*, and to a "hybrid" category if they were $2/3$ heterozygotes. A number of other allozymes have distributions correlated with the genetic species (Tables 7,8). Two are restricted to *D. globosa* and 12 to *D. harrisi*. No individual in any spring was identified as a potential F_1 hybrid so that the genetic isolation between the species is nearly complete. When individuals are allocated to genetic species and samples pooled within spring groups there is a complete separation of *D. globosa* and *D. harrisi* in phenetic trees (Figs 23, 24).

Summaries of genetic variation within samples are given in Tables 4-6, which detail the average number of individuals scored per locus, the percentage of loci with more than one allele and observed and expected heterozygosity. These summaries show a notable level of genetic variation in *Dalhousia*, with most samples having multiple alleles at more than 20% of loci. The *D. globosa* sample from the Ca1 pool (topotypic population) has multiple alleles at 53% of loci. Some samples with low variability are intriguing. Ca8 is one of the two springs where there is evidence of significant hybridization between *D. globosa* and *D. harrisi*. Yet it has the lowest percentage of polymorphic loci among the populations of *D. globosa* and one of the lowest seen in *D. harrisi*, accompanied by a low value in the "hybrids" class. Polymorphic loci are quite frequent in Cd2, the other spring where hybridization is occurring.

The genetic isolation between *D. globosa* and *D. harrisi* is emphasized by their wide sympatry within the springs. This criterion is not available for decisions regarding the specific status of lineages within the two nominate genetic species. Of particular interest here, is the population in a hot spring near Ca1, Ca1a (stn D24). This is an outlier to the other samples of *D. globosa* in phenograms (Figs 23, 24), principally because of a very high frequency of ALKP 3, LGG-2 2, SDH-1 2 and SDH-2 1 allozymes and the fixation of an unique GAL allozyme (3). The SDH phenotype is similar to *D. harrisi*. The three other characteristic allozymes of this hot spring population are absent or in very low frequencies in *D. harrisi*, contradicting a hybrid origin. It appears more likely that the

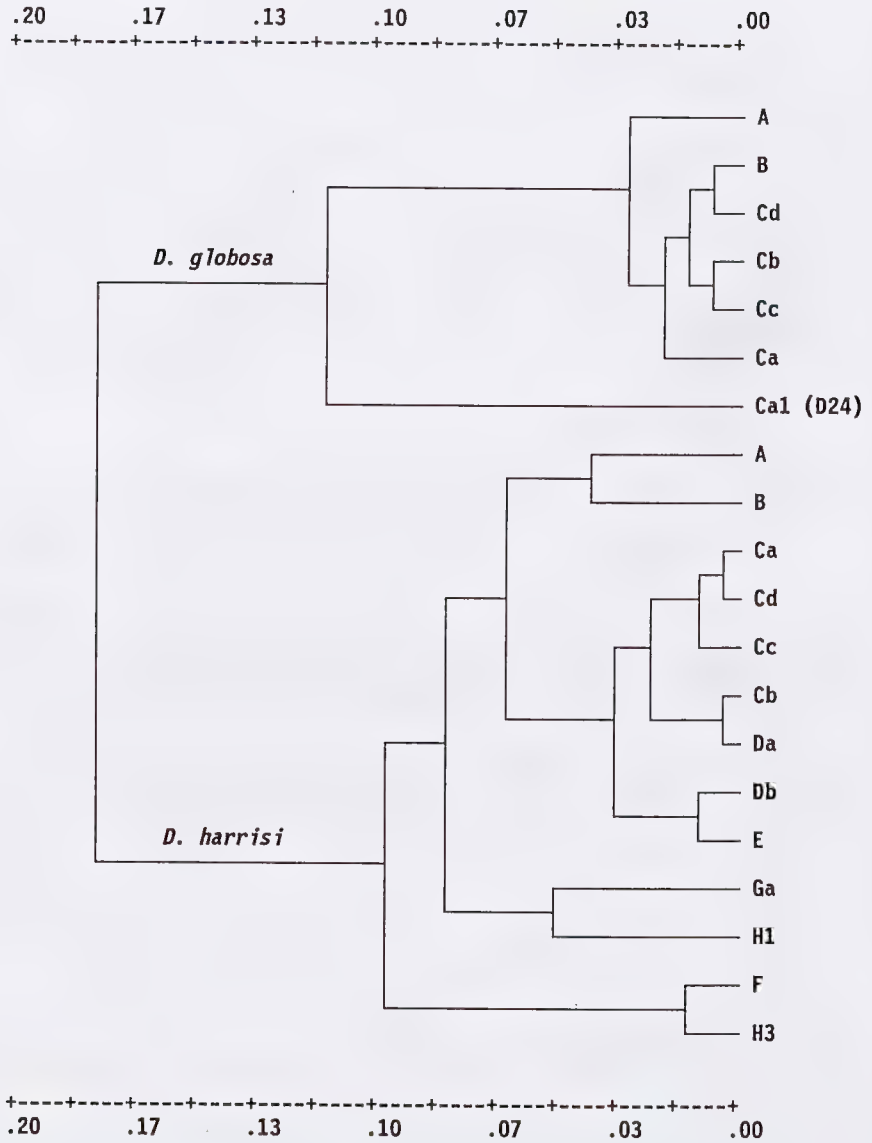


Figure 23. Phenogram showing relationships of *Dalhousia* based on unweighted pair group (UPGMA) clustering of Nei's unbiased (Nei, 1978) genetic distances between samples pooled into spring groups. *D. globosa* Ca1a (D24) and *D. harrisi* H1 and H3 samples have been treated separately, as suggested by inspection of their genetic frequencies.

D24 population has been sufficiently isolated from *D. globosa* populations for long enough to evolve large allelic frequency differences and, in at least this one example, novel allozymes. This population has the shell features of *D. harrisi* (Fig. 3E,H), there being no significant ($P < 0.01$) differences in shell dimensions and ratios. However, members of this sample tend to fall in the overlap zone between the two species (Fig. 22B).

Figure 23 shows that the distribution of genetic variation in *Dalhousia* is not random. The genetic distance between populations pooled in spring groups is generally concordant with the degree of

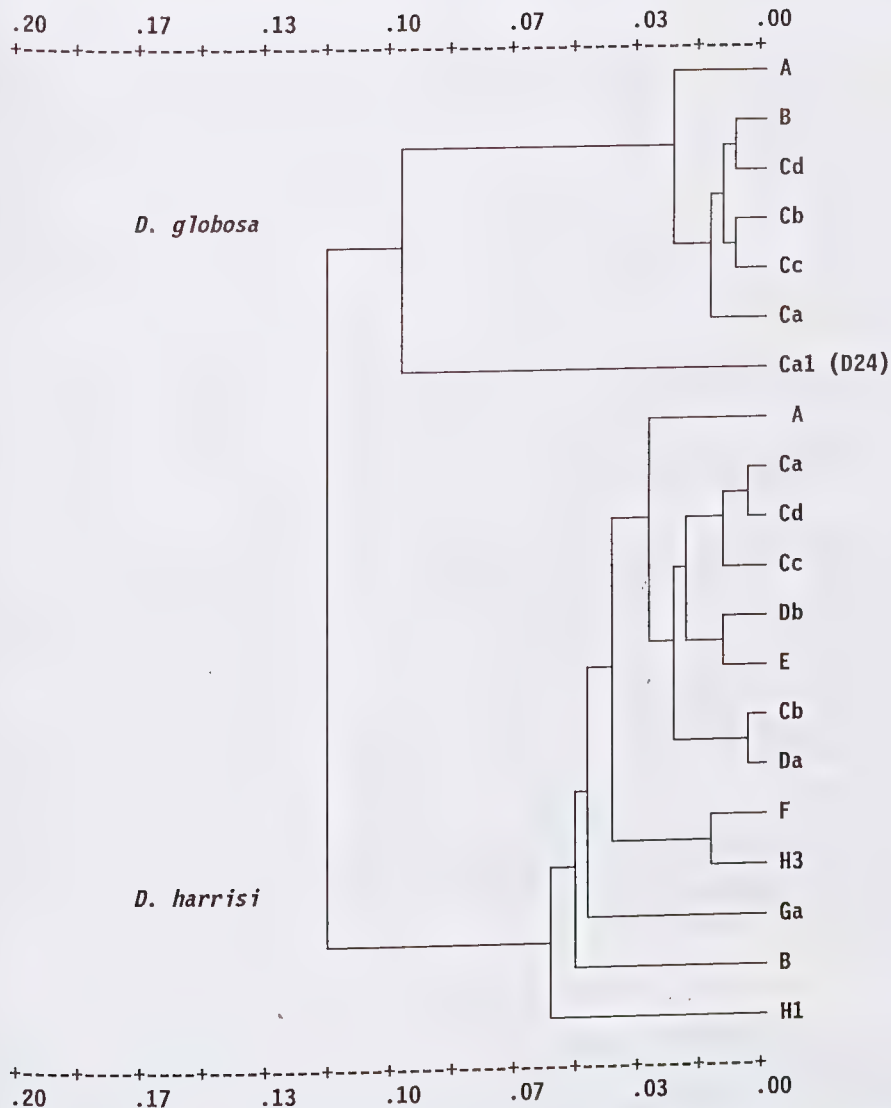


Figure 24. Phenogram showing relationships of *Dalhousia* based on complete linkage clustering of Nei's unbiased (Nei, 1978) genetic distances between samples pooled into spring groups. *D. globosa* Ca1a (D24) and *D. harrisi* H1 and H3 samples have been treated separately, as suggested by inspection of their genetic frequencies.

geographic separation, particularly in *D. harrisi*. Clear exceptions to this are the high degree of divergence of the Ca1a (D24) sample from the remainder of *D. globosa* and the low divergence between the F spring group and the geographically distant H3 spring in *D. harrisi*. In *D. harrisi*, spring group B is quite basal when UPGMA linkage is used for the clustering (Fig. 23). If, however, the phenogram is based on "complete" linkages, the pooled sample for B is the sister to A (Fig. 24). Phenograms (e.g. Fig. 23) reveal a number of lineages in *D. harrisi* characterised by frequency differences from other lineages within the species. Whilst there are no examples of fixed allozymic differences, some polymorphic loci have allozymes restricted to particular geographic areas. The prime example is the β -GAL 1 allozyme which is, with the exception of low frequencies in A1 and A2, found in the southern and southeastern springs. Other instances include the LGG-1 2 allozyme

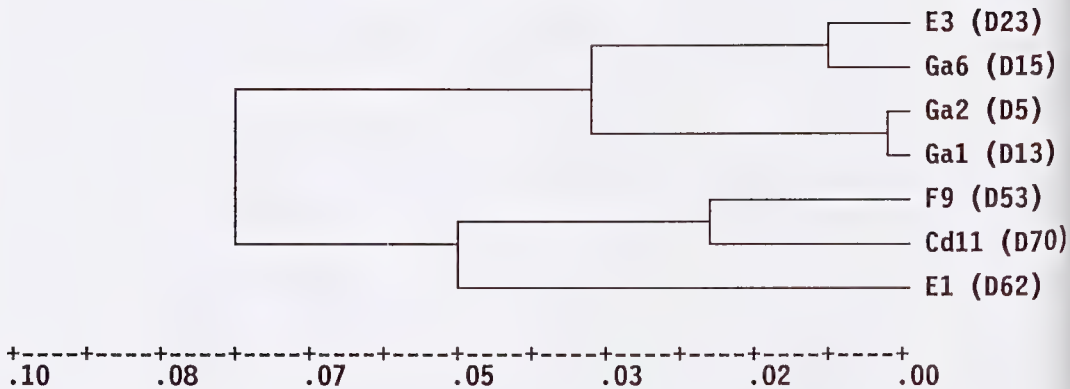


Figure 25. Phenogram showing relationships between populations of *Fluvidona centralia* based on an unweighted pair group (UPGMA) clustering of Nei's unbiased (Nei, 1978) genetic distances.

which is usually absent from the C and D spring groups, the ADH 4 allozyme with a disjunct distribution in groups A and H and the HK 3 allozyme concentrated in B and the adjacent Db groups.

Sample sizes are small in *F. centralia*, yet the apparent low levels of variation in this species (Table 6) probably reflect its biology, implying smaller founding populations and longer periods of isolation than in *Dalhousia*. There are two principal lineages within the species (Fig. 25), these characterised by a fixed-difference in *Gpt-2*. This may reflect a significant biological division of geographic variation within the taxon as we recognise it. There are no other allozymes with distributions concordant with the *Gpt-2* pattern although there are some loci (such as *Pgd*) with allozymes found only in some populations of one of the two lineages. The shell morphologies (Fig. 18; Table 3) of members of these two lineages do not differ greatly, there being no significant differences between any of the measurements for the pooled measured populations listed in each group. However, the ratios of shell width/shell length and aperture length/shell length were significantly different ($P < 0.001$; Fig. 21B) between the two groups for the subset of measured populations.

Discussion

Using the criterion of sympatry, we have recognised only two species-group taxa within *Dalhousia*. However, as outlined above, some of the lineages within both these species are genetically distinct, although allopatric, and both taxa show considerable intra and interpopulation variation in shell size and shape. Similarly within what we treat as a single species of *Fluvidona* there is considerable interpopulation variation in shell, opercular and radular morphology, as well as allopatric genetic subdivision.

The considerable variation seen in shell morphology in *Dalhousia* (Figs 2–5, 16, 17), briefly described above, will be analysed in more detail elsewhere.

As noted above, it is very likely that *Dalhousia* and *Fonscochlea*, from the Lake Eyre Supergroup, are sister taxa. The probable sister taxon to (*Fonscochlea* + *Dalhousia*) is *Jardinella* (Ponder and Clark, 1990), found in artesian springs in western Queensland, as well as in some coastal drainages in northern Queensland. Species of *Jardinella*, like most hydrobiids, have a normal bursa copulatrix and seminal receptacle. The presence of a single sperm sac (presumably the bursa copulatrix) in *Dalhousia* might appear to suggest that it is more derived than *Fonscochlea* which has two. However, the two sperm sacs of *Fonscochlea* are very similar histologically and may be the result of subdivision of an original single sperm sac (the bursa) (Ponder *et al.*, 1989). If this is the case, in this respect at least, *Dalhousia* is the more plesiomorphic of the two genera and in this genus the oviduct functions as a sperm storage site.

The presence of an endemic hydrobiid genus at Dalhousie Springs with a sister group in the Lake Eyre Springs raises questions about the origin and age of these taxa. Unfortunately there are few concrete data on the age of any of the springs associated with the Great Artesian Basin. The age of Dalhousie Springs has been discussed by Krieg (1989) who concludes that they are probably Pleistocene in age, being no older than 1–2 million years. Ponder (1986) has suggested that the Lake Eyre Supergroup springs contain such a differentiated fauna that they may well be Tertiary in age. If Dalhousie Springs are indeed Pleistocene in age, it is highly probable that *Dalhousia* is an immigrant to the springs from some other, now extinct, artesian spring group. It is possible (although unlikely), that *D. globosa* and *D. harrisi* had become specifically distinct before this immigration. Thus, in this scenario, the *Dalhousia* fauna of Dalhousie Springs would represent two colonization events. The presence of *F. centralia* indicates that multiple invasions of hydrobiids are possible and, indeed, cannot be discounted from our genetic data. The genetic differentiation of the D24 population from other samples of *D. globosa* has probably developed *in situ*, although, again, the possibility of a third colonization cannot be discounted. The genetic distance between D24 and *D. globosa* is comparable to that between *D. globosa* and *D. harrisi*, supporting the idea that there has been sufficiently long residence of *Dalhousia* at Dalhousie Springs for speciation to have occurred *in situ*.

The ancestry of *Fluvidona*, on the other hand, is probably not tied to artesian springs and this species may be an immigrant from some, probably now extinct habitat, or, possibly, the Flinders Ranges. It seems to us, however, that recent dispersal of such faunas between these two widely separated areas is less likely than immigration of the hydrobiids from nearby, previously suitable habitats, possibly in the early Pleistocene.

The phreatic amphipod at Dalhousie (Zeidler, 1991) is related to another surface species living in the springs, so may have evolved *in situ*. On the other hand, the surface amphipod (*Austrochiltonia* sp.) is similar to a species living in the Lake Eyre Supergroup springs and in many other aquatic habitats in southern Australia (Zeidler, 1989), although it is not known elsewhere in central Australia, except Edgbaston Springs in western Queensland (Ponder, 1986).

The evolution of the hydrobiids within Dalhousie Springs will be discussed in more detail elsewhere. Their great morphological plasticity may in part be coupled with their considerable genetic diversity. The interplay of factors in the physical and biological environment may also have a significant influence on shell morphology. There is a considerable range of physical factors such as spring size, water depth and temperature and biological factors are also probably important. Ponder (1989) suggested, for example, that the presence of the predatory catfish (*Neosilurus* sp.) in some of the large springs may result in the selection of larger, heavier-shelled individuals. Other biological factors, such as parasitism, can be significant in some springs.

Dalhousia globosa and *D. harrisi* maintain their genetic integrity over their range within the spring groups, clearly indicating that they are distinct species. Each may yet be found to represent a species complex, with the Ca1a (D24) sample of "*D. globosa*" being the most likely candidate. It may be noted, however, that gene flow in both *D. globosa* and *D. harrisi* is apparently high when pooled data are considered, with spring groups exchanging migrants at rates of the order of 20 individuals per spring group per generation (Colgan & Ponder, 1994). This level of gene flow would generally be sufficient to prevent fragmentation of *Dalhousia* into isolated, non-interbreeding species with very restricted ranges.

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Literature cited

- Boyd, W.E. 1990. Mound springs. Pp. 107–118. In: Tyler, M.J., Twidale, C.R., Davies, M. and Wells, C.B. Natural history of the North East deserts. Royal Society of South Australia, Adelaide.
- Colgan, D.J. and Ponder, W.F. 1994. The evolutionary consequences of restrictions in gene flow: examples from hydrobiid snails. *Nautilus*, Supplement 2: 25–43.
- Crowley, L.E.L.M. and Ivantsoff, W. 1990. A second hardyhead, *Craterocephalus gloveri* (Pisces: Atherinidae), from Dalhousie Springs, central Australia. *Ichthyological Exploration of Freshwaters* 1: 113–122.
- Department of the Environment, Sport and Territories (DEST), 1994. Australia's Biodiversity, an overview of selected significant components. Biodiversity Series, Paper No. 2, DEST, Canberra. 87pp.
- Glover, C.J.M. 1989. Fishes. Pp. 89–111. In: Zeidler, W. and Ponder, W.F. Natural History of Dalhousie Springs. Adelaide: South Australian Museum, Adelaide.
- Habermehl, M.A. 1982. Springs in the Great Artesian Basin – their origin and nature. Australian Bureau of Mineral Resources, Geology and Geophysics, Report 235.
- Harris, C. 1981. Oases in the desert: the mound springs of northern South Australia. *Royal Geographic Society of Australasia – South Australian Division, Proceedings* 81: 26–39.
- Harris, C. 1993. Mound springs: South Australian conservation initiatives. *Rangelands Journal* 14: 157–173.
- Hebert, P.D.N. and Beaton, M.J. 1989. Methodologies for allozyme analysis using cellulose acetate electrophoresis. Helena Laboratories, Austin.
- Hershler, R. 1985. Systematic revision of the Hydrobiidae (Gastropoda: Rissoacea) of the Cuatro Cie'negas Basin, Coahuila, Mexico. *Malacologia* 26: 31–123.
- Hershler, R. and Landye, J.J. 1988. Arizona Hydrobiidae (Prosobranchia: Rissoacea). *Smithsonian Contributions to Zoology* 459: 1–63.
- Hershler, R. and Sada, D.W. 1987. Springsnails (Gastropoda: Hydrobiidae) of Ash Meadows, Amargosa Basin, California-Nevada. *Proceedings of the Biological Society of Washington* 100: 776–843.
- Krieg, G.W. 1989. Geology. Pp. 19–26. In: Zeidler, W. and Ponder, W.F. Natural History of Dalhousie Springs. Adelaide: South Australian Museum, Adelaide.
- Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics* 89: 583–590.
- Ponder, W.F. 1985. South Australian mound springs: relict faunas in the desert. *Australian Natural History* 21: 352–255.
- Ponder, W.F. 1986. Mound springs of the Great Artesian Basin. Pp. 403–420. In: DeDecker, P. and Williams, W.D. *Limnology in Australia*. CSIRO, Melbourne.
- Ponder, W.F. 1989. Mollusca. Pp. 71–77. In: Zeidler, W. and Ponder, W.F. Natural History of Dalhousie Springs. Adelaide: South Australian Museum, Adelaide.
- Ponder, W.F. 1991. The eastern seaboard species of *Jardinella* (Mollusca, Gastropoda, Hydrobiidae), Queensland rainforest – inhabiting freshwater snails derived from the west. *Records of the Australian Museum* 43: 275–289.
- Ponder, W.F. 1994. Australian freshwater Mollusca – conservation priorities and indicator species. *Memoirs of the Queensland Museum* 36: 191–196.
- Ponder, W.F. 1995. Hydrobiid snails of the Great Artesian Basin. *Proceedings 9th International Malacological Congress*. IUCN special publication. In press.
- Ponder, W.F. and Clark, G.A. 1990. A radiation of hydrobiid snails in threatened artesian springs in western Queensland. *Records of the Australian Museum* 42: 301–363.
- Ponder, W.F., Clark, G.A., Miller, A. and Toluzzi, A. 1993. On a major radiation of freshwater snails in Tasmania and eastern Victoria – a preliminary overview of the *Beddomeia* group (Mollusca: Gastropoda: Hydrobiidae). *Invertebrate Taxonomy* 7: 501–750.
- Ponder, W.F., Colgan, D.J. and Clark, G.A. 1991. The morphology, taxonomy and genetic structure of *Tatea* (Mollusca: Gastropoda: Hydrobiidae), estuarine snails from temperate Australia. *Australian Journal of Zoology* 39: 447–497.
- Ponder, W.F., Colgan, D.J., Clark, G.A., Miller, A.C. and Terzis, T. 1994. Microgeographic genetic and morphological differentiation of freshwater snails – a study on the Hydrobiidae of Wilsons Promontory, Victoria, south eastern Australia. *Australian Journal of Zoology* 42: 557–678.
- Ponder, W.F., Egglar, P. and Colgan, D.J. 1995. Genetic differentiation of aquatic snails (Gastropoda: Hydrobiidae) from artesian springs in arid Australia. *Biological Journal of the Linnean Society*, in press.
- Ponder, W.F., Hershler, R. and Jenkins, B. 1989. An endemic radiation of hydrobiid snails from artesian springs in northern South Australia: Their taxonomy, physiology, distribution and anatomy. *Malacologia* 31: 1–140.
- Richardson, B.J., Baverstock, P.R. and Adams, M. 1986. *Allozyme Electrophoresis*. Academic Press, Sydney.
- Smith, P.C. 1989. Hydrogeology. Pp. 27–39. In: Zeidler, W. and Ponder, W.F. Natural History of Dalhousie Springs. Adelaide: South Australian Museum, Adelaide.

- Swofford, D.L. and Selander, R.B. 1989. Biosys-1. A computer program for the analysis of allelic variation in population genetics and biochemical systematics. Release 1.7. Illinois Natural History Survey, Champaign, IL.
- Wilkinson, L. 1992. SYSTAT for Windows. Version 5 Edition. SYSTAT Inc., Evanston, IL.
- Zeidler, W. 1989. Crustacea. Pp. 79–87. In: Zeidler, W. and Ponder, W.F. Natural History of Dalhousie Springs. Adelaide: South Australian Museum, Adelaide.
- Zeidler, W. 1991. A new genus and species of phreatic amphipod (Crustacea: Amphipoda) belonging in the "Chiltonia" generic group, from Dalhousie Springs, South Australia. Transactions of the Royal Society of South Australia 115: 177–187.
- Zeidler, W. and Ponder, W.F. (eds). 1989. Natural History of Dalhousie Springs. South Australian Museum, Adelaide.

APPENDICES

APPENDIX 1. Locality data for samples used for genetic analysis.

A general description of the springs and the nature of the habitat, as well as their hydrogeology, can be found in Zeidler and Ponder (1989). Most springs, including their outflows, are densely vegetated with *Phragmites* and *Melaleuca* being the most conspicuous vegetation. Many form mounds at the head of the spring, some several metres high. In all there are approximately 60 active springs in the Dalhousie Springs complex.

Abbreviations: Coll. – collectors:– DC – D. Colgan, DM – D. MacIntosh, JW – Janet Waterhouse, SC – Stephanie Clark, TT – T. Terzis, WP – W. Ponder. cond. – conductivity in mS cm^{-1} ; Stn – field station; temp. – water temperature. The species found are indicated in square brackets:– f – *F. centralia*, g – *D. globosa*, h – *D. harrisi*.

- A1, Stn. D04A, 26°23'10"S 135°32'05"E, medium spring, 30–40 m downstream from pool, pH 7.68, cond. 1.19, temp. 36°C, 4/5/1990, Coll. JW SC.[g,h]
- A2, Stn. D09, 26°23'12"S 135°32'02"E, large spring, in large pool at head, on mud in deeper water (large); on edges (small), pH 7.52, cond. 1.20, temp. 36°C, 4/5/1990, Coll. WP DC TT.[g,h]
- A3, Stn. D02A, 26°23'28"S 135°32'07"E, large spring, uppermost outflow, pH 7.37, cond. 1.19, temp. 41°C, 4/5/1990, Coll. JW SC DM. [h]
- A3, Stn. D02B, 26°23'12"S 135°32'07"E, head of spring (not a pool), pH 7.37, cond. 1.19, temp. 41°C, 4/5/1990, Coll. JW SC DM. [g]
- A6, Stn. D10, 26°23'22"S 135°31'58"E, seep, pH 7.73, cond. 1.88, temp. 27.5°C, 4/5/1990, Coll. WP. [h]
- A8, Stn. D11, 26°22'58"S 135°32'07"E, small active spring, pH 7.25, cond. 1.15, temp. 38°C, 4/5/1990, Coll. DC TT. [g,h]
- B1, Stn. D73, 26°24'53"S 135°31'35"E, large spring, upper outflow, root mats at edges of water where water is cooler, pH 7.56, cond. 1.13, temp. 41°C, 9/5/1990, Coll. DC SC. [g,h]
- B2, Stn. D74, 26°24'48"S 135°31'36"E, medium spring, upper outflow, pH 7.63, cond. 1.21, temp. 33°C, 9/5/1990, Coll. DC SC. [h]
- Ca1a, Stn. D24, hot spring flowing into head of spring Ca1, 26°24'29"S 135°31'07"E, on edges, pH 7.63, cond. 1.54, temp. 42°C, 7/5/1990, Coll. SC TT. [g]
- Ca1, Stn. D25, 26°24'30"S 135°31'07"E, very large spring, main pool, small species on edge of water, large species at edge and deeper, pH 7.51, cond. 1.55, temp. 40°C, 7/5/1990, Coll. SC TT. [g,h]
- Ca1, Stn. D26, 26°24'30"S 135°31'08"E, uppermost outflow, pH 7.84, cond. 1.70, temp. 38°C, 7/5/1990, Coll. SC TT. [g]
- Ca1, Stn. D27, 26°24'14"S 135°31'17"E, outflow 900m from pool, pH 7.40, cond. 1.71, temp. 36°C, 7/5/1990, Coll. SC TT. [g]
- Ca1, Stn. D28, 26°24'16"S 135°31'14"E, outflow 600m from pool, pH 7.86, cond. 1.78, temp. 37°C, 7/5/1990, Coll. SC TT. [g]
- Ca1, Stn. D46, outflow 200m from pool, 26°24'25"S 135°31'10"E, all over, pH 7.65, cond. 1.65, temp. 38°C, 7/5/1990, Coll. SC TT. [g]
- Ca2, Stn. D78, 26°24'26"S 135°30'58"E, medium spring flowing into Ca1, upper outflow, pH 7.65, cond. 1.81, temp. 42°C, 10/5/1990, Coll. JW. [h]

- Ca3, Stn. D76, 26°24'21"S 135°30'51"E, small active spring, at spring head, pH 7.20, cond. 1.51, temp. 29°C, 10/5/1990, Coll. JW DM. [h]
- Ca5, Stn. D75, "Duck Pond", 26°24'19"S 135°30'43"E, large circular pool, pH 7.62, cond. 1.25, temp. 34°C, 10/5/1990, Coll. JW DM. [h]
- Ca7, Stn. D34, 26°24'40"S 135°30'50"E, small trickle at spring head, pH 6.24, cond. 8.52, temp. 26°C, 7/5/1990, Coll. WP. [h]
- Ca7, Stn. D35, 26°24'26"S 135°31'01"E, medium spring, upper outflow, pH 7.73, cond. 2.67, temp. 27°C, 7/5/1990, Coll. WP. [h]
- Ca8, Stn. D38, a very small seep very near spring Ca8 and about 60 m W of western end of Ca1 pool. 26°24'27"S 135°31'00"E, on mud, pH 7.38, cond. 4.88, temp. 26°C, 7/5/1990, Coll. WP DM. [h]
- Ca8, Stn. D77, 26°24'25"S 135°31'02"E, small pool at head of medium spring, pH 7.66, cond. 1.50, temp. 43°C, 10/5/1990, Coll. JW. [g,h]
- Ca9, Stn. D64, 26°24'06"S 135°31'14"E, outflow of medium spring, pH 7.20, cond. 1.20, temp. 38.5°C, 8/5/1990, Coll. SC TT. [g]
- Ca11, Stn. D33, 26°24'34"S 135°30'49"E, seepage in channel, pH 7.69, cond. 2.60, temp. 23°C, 6/5/1990, Coll. WP. [h]
- Ca12, Stn. D36, 26°24'36"S 135°30'44"E, seepage on mound, pH 7.27, cond. 2.10, temp. 34.5°C, 7/5/1990, Coll. WP. [h]
- Cb2, Stn. D51, 26°25'25"S 135°30'27"E, main pool of large spring, pH 7.35, cond. 1.81, temp. 36°C, 8/5/1990, Coll. JW DM. [g]
- Cb2, Stn. D52, 26°25'22"S 135°30'28"E, small pond above main pool, pH 7.09, cond. 2.35, temp. 40.5°C, 8/5/1990, Coll. JW. [g]
- Cb4, Stn. D81, 26°25'44"S 135°31'15"E, small, active spring, spring head, pH 7.40, cond. 0.98, temp. 37°C, 10/5/1990, Coll. WP TT. [h]
- Cb5, Stn. D48, 26°25'56"S 135°30'12"E, small trickle, at head, pH 7.04, cond. 3.50, temp. 20°C, 8/5/1990, Coll. JW. [h]
- Cb5, Stn. D49, 26°25'55"S 135°30'13"E, upper middle outflow, small spring, pH 7.30, cond. 2.59, temp. 21°C, 8/5/1990, Coll. JW. [h]
- Cc1, Stn. D59, 26°25'13"S 135°29'33"E, pool at head of large spring, pH 7.45, cond. 2.47, temp. 38.5°C, 8/5/1990, Coll. WP DC. [g,h]
- Cc3, Stn. D61, 26°25'47"S 135°29'24"E, pool at head of very large spring, small species on edge, large species down to 2m+, pH 7.45, cond. 1.68, temp. 39°C, 9/5/1990, Coll. WP TT. [g,h]
- Cc4, Stn. D57, 26°24'10"S 135°29'20"E, large spring, in upper outflow, pH 7.60, cond. 1.45, temp. 38°C, 8/5/1990, Coll. WP, DC. [h]
- Cc8, Stn. D69, 26°25'48"S 135°29'54"E, small trickle on large mound, upper outflow, pH 7.30, cond. 2.72, temp. 24°C, 9/5/1990, Coll. DC SC. [h]
- Cd1, Stn. D40, 26°25'00"S 135°30'19"E, large spring, in below head, small species on edge, large species throughout pool, pH 7.12, cond. 1.55, temp. 36°C, 7/5/1990, Coll. WP DM. [h,g]
- Cd1, Stn. D41, 26°24'58"S 135°30'20"E, head of spring, in outflow of small hot spring flowing into main pool, pH 7.75, cond. 1.39, temp. 39.5°C, 7/5/1990, Coll. WP. [g]
- Cd1, Stn. D42, 26°24'58"S 135°30'21"E, upper outflow 100m down from pool, pH 7.67, cond. 1.45, temp. 35°C, 7/5/1990, Coll. WP. [g]
- Cd1, Stn. D43, 26°24'57"S 135°30'21"E, middle outflow, 250m from pool, pH 7.79, cond. 1.46, temp. 34.5°C, 7/5/1990, Coll. WP. [g]
- Cd2, Stn. D80, 26°24'12"S 135°30'12"E, very large spring, pool at head, pH 7.89, cond. 1.31, temp. 33°C, 10/5/1990, Coll. WP TT. [g,h]
- Cd3, Stn. D79, 26°24'19"S 135°30'06"E, small seep, at head, pH 7.32, cond. 1.45, temp. 34°C, 10/5/1990, Coll. WP TT. [h]
- Cd5, Stn. D63, 26°24'38"S 135°30'06"E, small spring, at head, pH 7.24, cond. 1.35, temp. 39°C, 10/5/1990, Coll. WP TT. [h]
- Cd8, Stn. D72, 26°24'50"S 135°30'24"E, large spring, upper outflow, pH 7.70, cond. 1.30, temp. 40°C, 9/5/1990, Coll. DC SC. [g]
- Cd9, Stn. D71, 26°24'48"S 135°30'24"E, seepage on large mound, pH 7.63, cond. 1.51, temp. 20°C, 9/5/1990, Coll. DC SC. [h]

- Cd11, Stn. D70, 26°24'40"S 135°30'29"E, small seepage on large mound, temp. 24°C, 9/5/1990, Coll. DC SC. [f]
- Da1, Stn. D56, 26°26'58"S 135°29'08"E, small seepage on large mound, pH 6.99, cond. 2.96, temp. 24°C, 8/5/1990, Coll. WP TT. [h]
- Da2, Stn. D45, 26°26'34"S 135°29'25"E, medium spring, small pool in upper outflow, pH 7.38, cond. 1.57, temp. 32°C, 8/5/1990, Coll. JW DM. [h]
- Da3, Stn. D44, 26°26'34"S 135°29'33"E, medium spring, upper outflow, pH 6.51, cond. 1.57, temp. 34.5°C, 8/5/1990, Coll. JW DM. [h]
- Db1, Stn. D31, 26°26'56"S 135°30'02"E, small seepage on large mound, temp. 24.5°C, 6/5/1990, Coll. WP DC. [h]
- Db2, Stn. D20, 26°27'15"S 135°30'12"E, large spring, near head, pH 6.66, cond. 2.06, temp. 31°C, 6/5/1990, Coll. WP DC. [h]
- Db4, Stn. D29A, 26°27'22"S 135°30'24"E, cold seep on large mound, pH 6.96, cond. 1.91, temp. 28°C, 6/5/1990, Coll. WP DC. [h]
- E1, Stn. D06, 26°29'52"S 135°30'09"E, medium spring, upper outflow, pH 7.82, cond. 1.60, temp. 30°C, 5/5/1990, Coll. JW SC. [h]
- E1, Stn. D62, 26°29'51"S 135°30'09"E, lower swampy outflow, pH 7.81, cond. 1.75, temp. 16.5°C, 9/5/1990, Coll. WP TT. [f]
- E2, Stn. D07, 26°30'06"S 135°30'04"E, small spring, at head, pH 7.80, cond. 1.86, temp. 31°C, 5/5/1990, Coll. JW SC. [h]
- E3, Stn. D23A, 26°28'08"S 135°29'42"E, small trickle, spring head, pH 7.11, cond. 5.46, temp. 22°C, 6/5/1990, Coll. JW DM. [f]
- E3, Stn. D23B, 26°28'04"S 135°29'41"E, about 20m from D23A, in open boggy area, pH 7.11, cond. 5.46, temp. 19°C, 6/5/1990, Coll. JW DM. [f]
- E5, Stn. D08, 26°29'08"S 135°29'38"E, small active spring, pH 7.18, cond. 1.80, temp. 25°C, 6/5/1990, Coll. JW DM. [h]
- E7, Stn. D17A, 26°29'47"S 135°30'00"E, small warm seep on large mound, pH 7.5, cond. 2.7, temp. 31°C, 5/5/1990, Coll. WP DC. [h]
- E8, Stn. D18, 26°29'47"S 135°29'55"E, small seep on large mound, on wet mud, temp. 25°C, 5/5/1990, Coll. WP DC. [h]
- F1, Stn. D54, 26°30'54"S 135°29'11"E, small active spring on large mound, at head, pH 7.20, cond. 1.81, temp. 21°C, 8/5/1990, Coll. WP. [h]
- F2, Stn. D55, 26°30'37"S 135°29'24"E, small active spring, upper outflow, pH 7.07, cond. 1.18, temp. 28°C, 8/5/1990, Coll. WP. [h]
- F9, Stn. D53, 26°31'06"S 135°29'15"E, small seep, pH 6.45, cond. 1.91, temp. 20°C, 8/5/1990, Coll. WP DC. [f]
- Ga1, Stn. D13, 26°31'36"S 135°29'59"E, small seep, pH 7.5, cond. 2.39, temp. 16°C, 5/5/1990, Coll. DC TT. [f]
- Ga2, Stn. D05A, 26°31'39"S 135°29'58"E, medium spring, in pool at head, pH 6.80, cond. 1.96, temp. 31°C, 5/5/1990, Coll. JW SC. [h]
- Ga2, Stn. D05B, 26°31'42"S 135°29'59"E, middle outflow, pH 7.30, cond. 2.06, temp. 20°C, 5/5/1990, Coll. JW SC. [f]
- Ga3, Stn. D14, 26°31'27"S 135°30'00"E, medium spring, pool at head, pH 7.33, cond. 2.57, temp. 34°C, 5/5/1990, Coll. WP DC TT. [h]
- Ga4, Stn. D12, 26°31'35"S 135°29'59"E, small seep on large mound, temp. 20°C, 5/5/1990, Coll. DC TT. [h]
- Ga6, Stn. D15, 26°31'05"S 135°30'01"E, small seepage on medium mound, pH 7.35, cond. 6.26, temp. 21°C, 5/5/1990, Coll. WP DC. [f]
- Ga6, Stn. D16, 26°31'06"S 135°30'03"E, small trickle, pH 7.48, cond. 2.19, temp. 35.5°C, 5/5/1990, Coll. WP DC. [h]
- H1, Stn. D01, 26°33'43"S 135°28'47"E, small active spring, medium mound, pH 7.24, cond. 2.02, temp. 24°C, 4/5/1990, Coll. WP DC JW SC. [h]
- H3, Stn. D19, Emily Springs, 26°33'23"S 135°27'15"E, large spring, upper outflow, pH 6.71, cond. 1.89, temp. 22°C, 6/5/1990, Coll. WP DC. [h]

APPENDIX 2

Measurement tables for shells

Table 2. Means and standard deviations (below) of shell measurements and ratios for *Dalhousia globosa* and *D. harrisi*.

<i>Dalhousia globosa</i>										
	SL	SW	AL	AW	BW	SW/SL	AW/AL	AL/SL	BW/SL	AW/SW
Spring A1 (D4A), Female, N=58	3.40	2.62	1.87	1.66	2.86	0.77	0.89	0.55	0.85	0.63
	0.55	0.39	0.29	0.23	0.43	0.04	0.05	0.03	0.03	0.02
Male, N=35	3.34	2.54	1.79	1.60	2.78	0.76	0.90	0.54	0.83	0.63
	0.45	0.30	0.22	0.18	0.35	0.04	0.04	0.03	0.05	0.02
Spring A2 (D9), Female, N=28	4.27	3.17	2.25	1.98	3.53	0.74	0.88	0.53	0.83	0.63
	0.19	0.13	0.10	0.09	0.15	0.03	0.03	0.02	0.02	0.02
Male, N=27	4.08	3.06	2.17	1.88	3.37	0.75	0.87	0.53	0.83	0.61
	0.30	0.22	0.16	0.13	0.22	0.04	0.05	0.02	0.01	0.02
Spring A3 (D2B), Female, N=27	2.51	1.74	1.27	1.17	2.04	0.70	0.92	0.51	0.81	0.67
	0.24	0.17	0.13	0.11	0.19	0.03	0.04	0.03	0.02	0.02
Male, N=25	2.48	1.72	1.23	1.16	2.00	0.69	0.94	0.50	0.81	0.68
	0.22	0.15	0.10	0.09	0.17	0.03	0.03	0.02	0.02	0.02
Spring Ca1 (D25, D26, D28, D46), Female, N=119	2.81	2.21	1.55	1.42	2.40	0.79	0.91	0.56	0.86	0.64
	0.72	0.56	0.40	0.37	0.58	0.05	0.05	0.05	0.03	0.03
Male, N=81	2.70	2.12	1.47	1.36	2.32	0.79	0.93	0.54	0.86	0.64
	0.64	0.50	0.36	0.33	0.51	0.03	0.04	0.03	0.02	0.03
Spring Ca1a (D24), Female, N=5	2.83	1.98	1.44	1.25	2.29	0.70	0.87	0.51	0.81	0.63
	0.21	0.17	0.14	0.12	0.20	0.02	0.04	0.02	0.03	0.02
Male, N=6	2.79	1.88	1.38	1.26	2.25	0.68	0.91	0.50	0.81	0.67
	0.38	0.24	0.18	0.14	0.30	0.03	0.03	0.02	0.02	0.02
Spring Ca9 (D64), Female, N=16	2.77	1.86	1.30	1.25	2.21	0.67	0.96	0.47	0.79	0.67
	0.29	0.22	0.15	0.14	0.24	0.04	0.03	0.02	0.02	0.03
Male, N=34	2.58	1.73	1.22	1.17	2.06	0.67	0.96	0.47	0.80	0.68
	0.29	0.17	0.14	0.11	0.20	0.04	0.05	0.02	0.02	0.03
Spring Cb2 (D51, D52), Female, N=52	2.90	2.11	1.50	1.34	2.42	0.73	0.90	0.52	0.83	0.64
	0.46	0.37	0.27	0.20	0.41	0.04	0.05	0.03	0.03	0.03
Male, N=57	2.86	2.11	1.51	1.34	2.41	0.74	0.90	0.53	0.84	0.64
	0.48	0.43	0.30	0.22	0.45	0.05	0.05	0.04	0.04	0.04
Spring Cc3 (D61), Female, N=30	3.23	2.48	1.72	1.53	2.69	0.77	0.89	0.53	0.83	0.62
	0.29	0.22	0.17	0.13	0.22	0.04	0.05	0.03	0.02	0.02
Male, N=25	3.08	2.34	1.61	1.47	2.56	0.76	0.91	0.52	0.83	0.63
	0.22	0.18	0.12	0.10	0.18	0.03	0.04	0.03	0.02	0.03
Spring Cd1 (D40-D43), Female, N=143	3.24	2.47	1.74	1.54	2.70	0.77	0.89	0.54	0.84	0.63
	0.70	0.48	0.32	0.28	0.55	0.05	0.04	0.04	0.03	0.02
Male, N=69	3.29	2.48	1.74	1.56	2.72	0.76	0.90	0.53	0.83	0.63
	0.69	0.47	0.34	0.28	0.52	0.04	0.05	0.03	0.03	0.03

Dalhousie Springs hydrobiids

	SL	SW	AL	AW	BW	SW/SL	AW/AL	AL/SL	BW/SL	AW/SW
<i>Dalhousia harrisi</i>										
Spring A2 (D9), Female, N=49										
	2.88	1.88	1.35	1.29	2.30	0.65	0.96	0.47	0.80	0.69
	0.26	0.17	0.14	0.10	0.20	0.03	0.06	0.02	0.02	0.03
Male, N=54										
	2.65	1.73	1.24	1.19	2.11	0.65	0.96	0.47	0.80	0.69
	0.30	0.20	0.15	0.13	0.23	0.03	0.04	0.02	0.02	0.03
Spring A3 (D2A), Female, N=28										
	2.80	1.79	1.27	1.25	2.17	0.64	0.98	0.46	0.78	0.70
	0.23	0.15	0.11	0.11	0.14	0.03	0.05	0.02	0.02	0.03
Male, N=27										
	2.69	1.70	1.21	1.20	2.06	0.63	0.99	0.45	0.77	0.70
	0.15	0.10	0.06	0.08	0.10	0.03	0.05	0.02	0.02	0.03
Spring A6 (D10), Female, N=12										
	2.95	1.87	1.36	1.25	2.27	0.64	0.92	0.46	0.77	0.67
	0.18	0.15	0.14	0.11	0.14	0.02	0.05	0.03	0.02	0.03
Male, N=13										
	2.80	1.83	1.33	1.22	2.17	0.65	0.92	0.46	0.78	0.67
	0.15	0.07	0.07	0.06	0.09	0.03	0.04	0.02	0.02	0.02
Spring B2 (D74), Female, N=19										
	2.90	1.86	1.34	1.27	2.26	0.64	0.96	0.46	0.78	0.69
	0.49	0.31	0.24	0.20	0.35	0.03	0.05	0.02	0.02	0.04
Male, N=36										
	2.74	1.75	1.26	1.18	2.13	0.64	0.94	0.46	0.78	0.68
	0.55	0.29	0.23	0.16	0.36	0.04	0.06	0.02	0.03	0.04
Spring Ca1 (D25), Female, N=22										
	2.80	2.01	1.44	1.35	2.29	0.72	0.94	0.51	0.82	0.67
	0.23	0.15	0.11	0.10	0.17	0.04	0.04	0.02	0.02	0.04
Male, N=28										
	2.79	1.96	1.42	1.33	2.27	0.70	0.93	0.51	0.81	0.68
	0.28	0.16	0.13	0.11	0.20	0.03	0.04	0.02	0.02	0.03
Spring Ca2 (D78), Female, N=22										
	2.44	1.55	1.13	1.12	1.90	0.64	0.99	0.46	0.78	0.72
	0.25	0.14	0.12	0.13	0.16	0.03	0.05	0.03	0.03	0.03
Male, N=28										
	2.30	1.45	1.06	1.05	1.80	0.63	0.99	0.46	0.78	0.73
	0.22	0.12	0.10	0.11	0.14	0.02	0.04	0.02	0.03	0.04
Spring Ca3 (D76), Female, N=24										
	3.77	2.39	1.71	1.56	2.88	0.64	0.92	0.45	0.77	0.66
	0.69	0.42	0.30	0.25	0.46	0.04	0.05	0.03	0.02	0.03
Male, N=26										
	3.09	1.98	1.41	1.31	2.39	0.65	0.94	0.46	0.78	0.67
	0.59	0.31	0.24	0.18	0.38	0.04	0.04	0.02	0.03	0.03
Spring Ca5 (D75), Female, N=27										
	4.13	2.97	2.05	1.86	3.27	0.72	0.91	0.50	0.79	0.63
	0.53	0.41	0.27	0.21	0.38	0.03	0.05	0.02	0.02	0.03
Male, N=23										
	3.74	2.64	1.80	1.67	2.92	0.71	0.93	0.48	0.78	0.64
	0.53	0.41	0.25	0.22	0.37	0.03	0.03	0.02	0.02	0.03
Spring Ca7 (D34, D35), Female, N=42										
	3.57	2.19	1.58	1.49	2.69	0.62	0.95	0.45	0.76	0.68
	0.84	0.45	0.33	0.29	0.54	0.03	0.04	0.02	0.04	0.03
Male, N=58										
	3.31	2.06	1.47	1.40	2.52	0.63	0.96	0.45	0.77	0.69
	0.88	0.48	0.35	0.31	0.57	0.04	0.04	0.03	0.04	0.03
Spring Ca8 (D38, D77), Female, N=38										
	2.71	1.73	1.23	1.22	2.10	0.64	0.99	0.46	0.78	0.70
	0.38	0.20	0.18	0.17	0.26	0.04	0.07	0.03	0.04	0.04

	SL	SW	AL	AW	BW	SW/SL	AW/AL	AL/SL	BW/SL	AW/SW
	Male, N=38									
	2.48	1.64	1.14	1.14	1.95	0.66	1.00	0.46	0.79	0.69
	0.35	0.20	0.17	0.16	0.24	0.03	0.08	0.03	0.03	0.04
Spring Ca12 (D36), Female, N=25	2.77	1.74	1.29	1.23	2.17	0.63	0.95	0.47	0.78	0.70
	0.26	0.14	0.10	0.11	0.19	0.03	0.05	0.03	0.02	0.03
	Male, N=25									
	2.48	1.59	1.17	1.13	1.96	0.64	0.97	0.47	0.79	0.71
	0.28	0.14	0.13	0.12	0.20	0.03	0.04	0.02	0.02	0.03
Spring Cb4 (D81), Female, N=34	2.62	1.69	1.20	1.16	2.05	0.65	0.97	0.46	0.79	0.69
	0.20	0.12	0.10	0.07	0.13	0.02	0.05	0.01	0.02	0.02
	Male, N=21									
	2.37	1.56	1.10	1.07	1.87	0.66	0.98	0.47	0.79	0.69
	0.24	0.14	0.11	0.08	0.14	0.03	0.04	0.02	0.03	0.03
Spring Cb5 (D48, D49), Female, N=41	2.99	1.89	1.35	1.32	2.30	0.63	0.98	0.45	0.77	0.70
	0.37	0.22	0.16	0.14	0.24	0.02	0.05	0.02	0.03	0.03
	Male, N=64									
	2.70	1.72	1.24	1.22	2.11	0.64	0.99	0.46	0.78	0.71
	0.23	0.15	0.11	0.09	0.16	0.03	0.04	0.02	0.02	0.03
Spring Cc1 (D59), Female, N=24	2.57	1.67	1.22	1.16	2.05	0.65	0.95	0.48	0.80	0.70
	0.22	0.13	0.11	0.08	0.17	0.03	0.04	0.02	0.02	0.03
	Male, N=31									
	2.40	1.54	1.13	1.07	1.91	0.65	0.95	0.47	0.80	0.70
	0.32	0.16	0.12	0.12	0.21	0.05	0.04	0.03	0.03	0.03
Spring Cc3 (D61), Female, N=30	2.69	1.86	1.37	1.24	2.22	0.69	0.91	0.51	0.82	0.67
	0.26	0.15	0.13	0.09	0.19	0.03	0.04	0.02	0.02	0.03
	Male, N=25									
	2.62	1.83	1.34	1.23	2.15	0.70	0.92	0.51	0.82	0.67
	0.26	0.19	0.14	0.12	0.19	0.02	0.03	0.02	0.02	0.02
Spring Cc8 (D69), Female, N=31	2.91	1.82	1.31	1.28	2.23	0.63	0.98	0.45	0.77	0.70
	0.33	0.20	0.12	0.13	0.21	0.03	0.03	0.02	0.03	0.03
	Male, N=24									
	2.86	1.78	1.28	1.26	2.20	0.62	0.99	0.45	0.77	0.71
	0.21	0.10	0.10	0.07	0.15	0.02	0.05	0.02	0.02	0.02
Spring Cd1 (D40), Female, N=21	2.60	1.81	1.32	1.22	2.13	0.70	0.92	0.51	0.82	0.67
	0.19	0.13	0.10	0.09	0.15	0.04	0.04	0.02	0.02	0.02
	Male, N=34									
	2.54	1.84	1.28	1.20	2.07	0.73	0.94	0.50	0.82	0.67
	0.22	0.34	0.11	0.10	0.17	0.13	0.03	0.02	0.02	0.07
Spring Cd2 (D80), Female, N=24	2.74	1.97	1.39	1.28	2.25	0.72	0.92	0.51	0.82	0.65
	0.18	0.10	0.08	0.06	0.13	0.04	0.03	0.02	0.03	0.02
	Male, N=31									
	2.72	1.88	1.34	1.25	2.19	0.69	0.93	0.49	0.80	0.67
	0.22	0.15	0.10	0.09	0.16	0.03	0.03	0.02	0.02	0.02
Spring Cd3 (D79), Female, N=20	2.87	1.82	1.29	1.23	2.16	0.64	0.95	0.46	0.77	0.68
	0.51	0.21	0.15	0.12	0.23	0.08	0.04	0.06	0.09	0.03
	Male, N=24									
	2.40	1.60	1.16	1.07	1.90	0.67	0.92	0.48	0.79	0.67
	0.26	0.17	0.13	0.11	0.18	0.03	0.05	0.02	0.03	0.03

	SL	SW	AL	AW	BW	SW/SL	AW/AL	AL/SL	BW/SL	AW/SW
Spring Cd5 (D63), Female, N=40										
	2.79	2.17	1.28	1.22	2.16	0.64	0.96	0.46	0.78	0.68
	0.32	0.15	0.14	0.13	0.21	0.04	0.05	0.02	0.02	0.03
Male, N=65										
	2.58	1.67	1.20	1.15	2.02	0.65	0.96	0.47	0.79	0.69
	0.27	0.15	0.11	0.11	0.17	0.03	0.04	0.02	0.03	0.03
Spring Cd9 (D71), Female, N=28										
	3.54	2.17	1.52	1.42	2.61	0.61	0.93	0.43	0.74	0.65
	0.29	0.15	0.11	0.10	0.18	0.03	0.05	0.02	0.02	0.03
Male, N=27										
	3.44	2.07	1.50	1.37	2.55	0.60	0.91	0.44	0.74	0.66
	0.27	0.17	0.11	0.11	0.18	0.03	0.06	0.02	0.02	0.03
Spring Da2 (D5), Female, N=57										
	3.02	2.01	1.45	1.37	2.35	0.67	0.94	0.48	0.78	0.68
	0.32	0.18	0.15	0.12	0.23	0.03	0.05	0.02	0.02	0.03
Male, N=48										
	2.97	1.97	1.42	1.35	2.32	0.66	0.96	0.48	0.78	0.69
	0.32	0.21	0.17	0.13	0.23	0.02	0.05	0.02	0.02	0.03
Spring Da3a (D44), Female, N=22										
	3.00	1.94	1.41	1.30	2.30	0.65	0.92	0.47	0.77	0.67
	0.26	0.15	0.12	0.08	0.19	0.03	0.04	0.02	0.02	0.02
Male, N=33										
	2.95	1.89	1.40	1.29	2.28	0.64	0.92	0.48	0.77	0.68
	0.31	0.21	0.16	0.12	0.23	0.03	0.04	0.02	0.02	0.03
Spring Db1 (D31), Female, N=14										
	2.78	1.80	1.31	1.22	2.18	0.65	0.94	0.47	0.79	0.68
	0.28	0.16	0.14	0.11	0.19	0.03	0.05	0.02	0.02	0.02
Male, N=33										
	2.58	1.68	1.23	1.15	2.04	0.65	0.94	0.48	0.79	0.69
	0.27	0.16	0.13	0.10	0.19	0.02	0.05	0.02	0.02	0.03
Spring Db4a (D21, D29), Female, N=27										
	2.59	1.64	1.19	1.14	2.03	0.64	0.97	0.46	0.79	0.70 [†]
	0.31	0.16	0.13	0.13	0.22	0.03	0.04	0.02	0.02	0.03
Male, N=14										
	1.48	1.09	1.06	1.86	1.57	0.74	1.76	0.71	1.06	1.71
	0.10	0.07	0.08	0.09	0.51	0.02	0.07	0.03	0.35	0.06
Spring E1 (D6), Female, N=24										
	3.60	2.29	1.63	1.54	2.77	0.64	0.95	0.45	0.77	0.67
	0.34	0.23	0.17	0.13	0.25	0.03	0.05	0.02	0.02	0.03
Male, N=26										
	3.41	2.17	1.52	1.47	2.59	0.64	0.97	0.45	0.76	0.68
	0.44	0.29	0.22	0.16	0.32	0.03	0.05	0.02	0.02	0.03
Spring E2 (D7), Female, N=26										
	3.04	1.99	1.44	1.36	2.36	0.66	0.94	0.47	0.78	0.68
	0.31	0.21	0.16	0.12	0.23	0.03	0.05	0.02	0.02	0.03
Male, N=29										
	2.89	1.89	1.37	1.29	2.25	0.65	0.94	0.47	0.78	0.68
	0.26	0.17	0.14	0.12	0.21	0.02	0.04	0.02	0.02	0.03
Spring E5 (D8), Female, N=13										
	3.03	2.06	1.47	1.35	2.36	0.68	0.93	0.48	0.78	0.66
	0.49	0.29	0.26	0.14	0.36	0.03	0.07	0.02	0.02	0.03
Male, N=9										
	2.54	1.74	1.23	1.23	2.01	0.69	1.00	0.49	0.79	0.71
	0.33	0.20	0.14	0.21	0.23	0.02	0.14	0.02	0.02	0.10

	SL	SW	AL	AW	BW	SW/SL	AW/AL	AL/SL	BW/SL	AW/SW
Spring E7a (D17A), Female, N=32	2.86	1.72	1.26	1.22	2.14	0.60	0.97	0.44	0.75	0.71
	0.27	0.12	0.10	0.09	0.17	0.03	0.04	0.02	0.02	0.02
Male, N=18	2.61	1.62	1.18	1.15	2.00	0.62	0.98	0.45	0.77	0.71
	0.18	0.10	0.07	0.10	0.11	0.03	0.05	0.02	0.02	0.04
Spring E8 (D18), Female, N=25	2.91	1.74	1.27	1.26	2.19	0.60	1.00	0.44	0.75	0.73
	0.28	0.15	0.12	0.10	0.19	0.02	0.03	0.01	0.02	0.03
Male, N=25	2.84	1.73	1.24	1.21	2.15	0.61	0.98	0.44	0.76	0.70
	0.24	0.13	0.11	0.09	0.17	0.02	0.05	0.02	0.01	0.02
Spring F1 (D54), Female, N=46	3.44	2.18	1.57	1.43	2.62	0.63	0.91	0.46	0.76	0.66
	0.39	0.23	0.19	0.16	0.28	0.02	0.05	0.02	0.02	0.04
Male, N=58	3.34	2.07	1.51	1.37	2.51	0.62	0.91	0.45	0.75	0.66
	0.44	0.26	0.20	0.16	0.31	0.03	0.06	0.02	0.02	0.04
Spring Ga2 (D5), Female, N=27	2.51	1.61	1.16	1.07	1.99	0.64	0.92	0.47	0.80	0.67
	0.35	0.17	0.15	0.15	0.23	0.05	0.07	0.06	0.07	0.05
Male, N=23	2.27	1.48	1.04	0.98	1.79	0.65	0.96	0.46	0.79	0.67
	0.30	0.18	0.15	0.11	0.22	0.03	0.09	0.04	0.04	0.04
Spring Ga3a (D14), Female, N=22	3.10	1.93	1.38	1.32	2.31	0.62	0.96	0.44	0.74	0.69
	0.28	0.19	0.13	0.12	0.19	0.02	0.035	0.02	0.03	0.02
Male, N=28	2.90	1.82	1.29	1.26	2.19	0.63	0.97	0.45	0.76	0.69
	0.30	0.19	0.16	0.15	0.23	0.03	0.06	0.02	0.03	0.03
Spring Ga6b (D16), Female, N=50	3.07	1.97	1.47	1.29	2.41	0.64	0.88	0.48	0.79	0.66
	0.57	0.31	0.25	0.18	0.39	0.04	0.05	0.02	0.03	0.03
Male, N=52	2.64	1.73	1.30	1.16	2.12	0.66	0.90	0.49	0.81	0.67
	0.54	0.32	0.25	0.18	0.37	0.04	0.05	0.02	0.03	0.03
Spring H1 (D1), Female, N=28	3.13	1.99	1.41	1.34	2.40	0.64	0.95	0.45	0.77	0.68
	0.34	0.19	0.14	0.12	0.22	0.03	0.05	0.02	0.02	0.02
Male, N=27	2.88	1.90	1.30	1.27	2.22	0.66	0.976	0.45	0.77	0.67
	0.19	0.12	0.09	0.09	0.14	0.02	0.04	0.02	0.02	0.02
Spring H3 (D19), Female, N=13	3.35	2.10	1.51	1.42	2.55	0.63	0.94	0.45	0.76	0.68
	0.18	0.14	0.12	0.08	0.15	0.02	0.04	0.02	0.02	0.02
Male, N=12	3.35	2.03	1.46	1.40	2.51	0.61	0.96	0.44	0.75	0.69
	0.21	0.11	0.06	0.04	0.09	0.03	0.04	0.02	0.03	0.02

Table 3. Means and standard deviations (below) of shell measurements and ratios for *Fluvidona centralia*.

	SL	SW	AL	AW	BW	SW/SL	AW/AL	AL/SL	BW/SL	AW/SW
Spring Cd11 (D70), Female, N = 6	1.91	1.16	0.78	0.69	1.39	0.61	0.90	0.41	0.73	0.60
	0.16	0.07	0.08	0.05	0.13	0.03	0.03	0.02	0.03	0.02
Male, N=14	1.71	1.05	0.70	0.63	1.26	0.62	0.90	0.41	0.74	0.60
	0.11	0.07	0.06	0.06	0.09	0.03	0.06	0.02	0.02	0.03
Spring E1 (D62), Female, N=16	2.63	1.56	1.06	0.91	1.89	0.60	0.86	0.41	0.72	0.58
	0.22	0.12	0.09	0.07	0.15	0.03	0.05	0.03	0.03	0.03
Male, N=4	2.42	1.43	1.01	0.83	1.76	0.59	0.83	0.42	0.73	0.58
	0.12	0.07	0.07	0.01	0.08	0.02	0.05	0.03	0.03	0.03
Spring E3 (D23A), Female, N=18	2.45	1.54	1.05	0.88	1.80	0.63	0.84	0.43	0.74	0.57
	0.17	0.09	0.07	0.05	0.10	0.02	0.04	0.02	0.02	0.02
Male, N=2	2.22	1.35	0.92	0.78	1.58	0.61	0.85	0.41	0.71	0.57
	0.23	0.10	0.09	0.06	0.17	0.02	0.02	0.00	0.00	0.01
Spring F9 (D53), Female, N=14	2.20	1.36	0.92	0.80	1.59	0.62	0.87	0.42	0.72	0.59
	0.22	0.10	0.09	0.06	0.14	0.03	0.05	0.02	0.03	0.01
Male, N=5	2.26	1.33	0.90	0.76	1.60	0.59	0.85	0.40	0.71	0.58
	0.29	0.15	0.09	0.09	0.18	0.02	0.03	0.02	0.03	0.01
Spring Ga1 (D13), Female, N=10	2.11	1.37	0.93	0.81	1.61	0.65	0.87	0.44	0.76	0.59
	0.18	0.09	0.09	0.06	0.15	0.03	0.04	0.03	0.02	0.02
Male, N=10	1.86	1.17	0.80	0.70	1.40	0.63	0.88	0.43	0.75	0.59
	0.23	0.15	0.11	0.09	0.18	0.03	0.04	0.02	0.02	0.02
Spring Ga2A (D5), Female, N=16	2.90	1.76	1.26	1.00	2.11	0.61	0.80	0.43	0.73	0.57
	0.23	0.11	0.07	0.06	0.12	0.02	0.04	0.02	0.02	0.02
Male, N=3	3.15	1.78	1.30	1.02	2.24	0.57	0.78	0.41	0.71	0.57
	0.26	0.07	0.14	0.07	0.20	0.03	0.03	0.02	0.03	0.03

APPENDIX 3

Allozyme data

Table 4. Measures of genetic variation within samples of *Dalhousia globosa*. The columns give the mean sample size and mean number of alleles per locus, the percentage of loci where more than one allozyme was detected, the mean observed heterozygosity and Nei's (1978) unbiased estimate of expected heterozygosity. Standard deviations are given in brackets.

Population	Mean sample size per Locus	Mean no. of alleles per locus	Percentage of loci polymorphic	Mean heterozygosity	
				Direct-count	HdyWbg expected
1. D4A (A1)	6.6 (.2)	1.3 (.1)	21.9	.057 (.022)	.075 (.031)
2. D9 (A2)	6.0 (.2)	1.2 (.1)	12.5	.067 (.035)	.063 (.031)
3. D2A (A3)	8.3 (.5)	1.4 (.1)	28.1	.077 (.036)	.106 (.037)
4. D11a (A8)	19.2 (1.8)	1.5 (.1)	37.5	.043 (.015)	.084 (.027)
5. D73 (B1)	11.5 (1.3)	1.5 (.2)	34.4	.067 (.024)	.113 (.038)
6. D24 (Ca1a, hot spr)	13.9 (1.3)	1.2 (.1)	15.6	.018 (.008)	.021 (.009)
7. D25 (Ca1 pool)	54.5 (4.0)	1.8 (.2)	53.1	.046 (.016)	.099 (.030)
8. D26 (Ca1 outflow)	35.0 (4.0)	1.4 (.1)	28.1	.029 (.014)	.057 (.025)
9. D28 (Ca1 outflow)	31.4 (3.9)	1.3 (.1)	21.9	.043 (.019)	.066 (.028)
10. D46 (Ca1 outflow)	27.0 (3.1)	1.3 (.1)	18.8	.048 (.023)	.063 (.028)
11. D77 (Ca8)	10.1 (1.7)	1.2 (.1)	9.4	.015 (.015)	.043 (.028)
12. D77 hybrids	7.8 (1.0)	1.2 (.1)	12.5	.050 (.036)	.049 (.026)
13. D64 (Ca9)	30.3 (4.0)	1.3 (.1)	21.9	.028 (.015)	.064 (.029)
14. D51 (Cb2)	13.0 (.4)	1.4 (.1)	31.3	.068 (.024)	.092 (.031)
15. D52 (Cb2)	6.3 (.3)	1.4 (.1)	21.9	.075 (.033)	.107 (.039)
16. D59 (Cc1)	5.9 (.2)	1.2 (.1)	18.8	.071 (.032)	.097 (.036)
17. D61 (Cc3)	6.8 (.5)	1.3 (.1)	18.8	.090 (.042)	.079 (.033)
18. D40 (Cd1 pool)	9.0 (.5)	1.3 (.1)	18.8	.084 (.033)	.088 (.035)
19. D43 (Cd1)	7.4 (.4)	1.5 (.2)	28.1	.119 (.039)	.138 (.043)
20. D41 (Cd1 head)	7.3 (.3)	1.3 (.1)	18.8	.079 (.034)	.089 (.035)
21. D42 (Cd1 outflow)	4.5 (.2)	1.3 (.1)	25.0	.130 (.048)	.114 (.038)
22. D80 (Cd2)	6.5 (.8)	1.3 (.1)	21.9	.052 (.026)	.082 (.032)
23. D80 hybrids	9.6 (1.1)	1.5 (.1)	37.5	.101 (.037)	.119 (.035)
24. D72 (Cd8)	5.5 (.3)	1.2 (.1)	18.8	.055 (.027)	.054 (.024)

Table 5. Measures of genetic variation within samples of *Dalhousia harrisi*. The columns give the mean sample size and mean number of alleles per locus, the percentage of loci where more than one allozyme was detected, the mean observed heterozygosity and Nei's (1978) unbiased estimate of expected heterozygosity. Standard deviations are given in brackets.

Population	Mean sample size per Locus	Mean No. of alleles per locus	Percentage of loci polymorphic	Mean heterozygosity	
				Direct-count	HdyWbg expected
1. D4A (A1)	18.1 (1.8)	1.3 (.1)	28.1	.064 (.025)	.083 (.030)
2. D9 (A2)	20.5 (2.1)	1.3 (.1)	28.1	.048 (.020)	.060 (.024)
3. D2 (A3)	6.4 (.4)	1.2 (.1)	15.6	.044 (.023)	.048 (.023)
4. D10 (A6)	18.1 (1.8)	1.3 (.1)	18.8	.078 (.032)	.076 (.031)
5. D11b (A8)	5.0 (.3)	1.1 (.1)	9.4	.031 (.019)	.027 (.017)
6. D73 (B1)	7.9 (.8)	1.4 (.1)	31.3	.060 (.023)	.103 (.032)
7. D74 (B2)	9.5 (.3)	1.3 (.1)	25.0	.048 (.019)	.063 (.021)
8. DZ5 (Ca1 pool)	17.1 (1.9)	1.5 (.2)	28.1	.039 (.017)	.063 (.026)
9. D78 (Ca2)	27.0 (3.8)	1.3 (.1)	18.8	.027 (.015)	.043 (.025)
10. D76 (Ca3)	24.8 (3.4)	1.4 (.1)	28.1	.052 (.021)	.084 (.030)
11. D75 (Ca5)	31.9 (3.2)	1.3 (.1)	25.0	.051 (.025)	.071 (.033)
12. D34 (Ca7)	25.6 (3.9)	1.1 (.1)	3.1	.002 (.002)	.002 (.002)
13. D35 (Ca7)	27.8 (3.9)	1.1 (.1)	9.4	.004 (.003)	.022 (.016)
14. D38 (Ca8)	17.6 (1.8)	1.3 (.2)	12.5	.067 (.037)	.066 (.033)
15. D77 (Ca8)	7.5 (1.1)	1.2 (.1)	15.6	.025 (.018)	.063 (.029)
16. D36 (Ca12)	27.2 (3.9)	1.3 (.1)	18.8	.039 (.024)	.046 (.022)
17. D33 (Ca11)	25.8 (3.5)	1.3 (.1)	25.0	.045 (.023)	.064 (.028)
18. D81 (Cb4)	8.4 (.6)	1.2 (.1)	21.9	.060 (.028)	.061 (.025)
19. D48 (Cb5 head)	18.9 (2.1)	1.3 (.1)	18.8	.039 (.021)	.073 (.030)
20. D49 (Cb5 outflow)	6.0 (.1)	1.2 (.1)	18.8	.059 (.030)	.079 (.032)
21. D59 (Cc1)	6.3 (.2)	1.2 (.1)	21.9	.057 (.024)	.077 (.028)
22. D61 (Cc3)	8.0 (.5)	1.2 (.1)	12.5	.030 (.015)	.036 (.018)
23. D57 (Cc4)	16.5 (1.7)	1.2 (.1)	12.5	.027 (.016)	.043 (.023)
24. D69 (Cc8)	8.7 (.4)	1.2 (.1)	15.6	.027 (.015)	.053 (.025)
25. D40 (Cd1 pool)	6.9 (.3)	1.4 (.1)	31.3	.066 (.024)	.114 (.037)

Population	Mean sample size per Locus	Mean No. of alleles per locus	Percentage of loci polymorphic	Mean heterozygosity	
				Direct- count	HdyWbg expected
26. D80B (Cd2)	18.1 (2.5)	1.4 (.1)	31.3	.068 (.024)	.084 (.028)
27. D79 (Cd3)	5.5 (.2)	1.3 (.1)	21.9	.067 (.029)	.098 (.036)
28. D63 (Cd5)	5.4 (.1)	1.3 (.1)	21.9	.052 (.019)	.079 (.028)
29. D71 (Cd9)	6.4 (.3)	1.1 (.1)	12.5	.042 (.020)	.045 (.022)
30. D56 (Da1)	5.9 (.2)	1.2 (.1)	21.9	.040 (.020)	.076 (.029)
31. D45 (Da2)	17.9 (2.0)	1.2 (.1)	12.5	.036 (.019)	.072 (.035)
32. D44 (Da3)	11.8 (.4)	1.2 (.1)	18.8	.014 (.008)	.053 (.024)
33. D31 (Db1)	5.9 (.1)	1.3 (.1)	18.8	.026 (.017)	.082 (.032)
34. D20 (Db2)	9.5 (.3)	1.3 (.1)	31.3	.063 (.024)	.128 (.035)
35. D29 (Db4)	6.0 (.2)	1.2 (.1)	15.6	.020 (.012)	.062 (.031)
36. D6 (E1)	20.0 (1.6)	1.4 (.1)	34.4	.069 (.024)	.095 (.029)
37. D7 (E2)	8.8 (.3)	1.5 (.1)	34.4	.069 (.022)	.109 (.031)
38. D8 (E5)	23.3 (1.6)	1.3 (.1)	25.0	.031 (.013)	.036 (.015)
39. D17A (E7)	17.4 (1.3)	1.3 (.1)	25.0	.046 (.020)	.069 (.029)
40. D18 (E8)	21.4 (1.9)	1.3 (.1)	15.6	.042 (.020)	.069 (.033)
41. D54 (F1)	21.0 (1.8)	1.3 (.1)	25.0	.035 (.016)	.056 (.024)
42. D55 (F2)	17.4 (1.6)	1.3 (.1)	21.9	.043 (.019)	.067 (.029)
43. D5 (Ga2)	25.4 (2.2)	1.3 (.1)	31.3	.043 (.016)	.066 (.024)
44. D14 (Ga3)	32.8 (1.9)	1.3 (.1)	25.0	.058 (.025)	.060 (.026)
45. D12 (Ga4)	19.3 (1.9)	1.2 (.1)	15.6	.059 (.029)	.071 (.033)
46. D16 (Ga6)	19.9 (.5)	1.5 (.1)	37.5	.047 (.017)	.082 (.028)
47. D1 (H1)	19.5 (1.8)	1.3 (.1)	18.8	.037 (.021)	.069 (.029)
48. D19 (H3)	17.6 (1.6)	1.3 (.1)	21.9	.053 (.025)	.079 (.033)

Table 6. Measures of genetic variation within samples of *Fluvidona centralia*. The columns give the mean sample size and mean number of alleles per locus, the percentage of loci where more than one allozyme was detected, the mean observed heterozygosity and Nei's (1978) unbiased estimate of expected heterozygosity. Standard deviations are given in brackets.

Population	Mean sample size per Locus	Mean No. of alleles per locus	Percentage of loci polymorphic	Mean heterozygosity	
				Direct- count	HdyWbg expected
1. D70 (Cd11)	3.7 (.2)	1.0 (.0)	4.0	.020 (.020)	.017 (.017)
2. D62 (E1 outflow)	11.7 (.2)	1.0 (.0)	.0	.000 (.000)	.000 (.000)
3. D23A&B (E3)	12.9 (.5)	1.0 (.0)	.0	.000 (.000)	.000 (.000)
4. D53 (F9)	9.3 (.4)	1.0 (.0)	4.0	.003 (.003)	.003 (.003)
5. D13 (Ga1)	12.0 (.0)	1.1 (.1)	12.0	.027 (.016)	.048 (.027)
6. D5 outflow (Ga2)	12.0 (.0)	1.2 (.1)	16.0	.053 (.026)	.062 (.030)
7. D15 (Ga6)	4.0 (.0)	1.0 (.0)	4.0	.020 (.020)	.023 (.023)

Table 7. Gene frequency data for *Dalhousia globosa*. The number of scored individuals follows the locus name. Identifiable hybrids are listed separately in Ca8 and Cd2.

Spring Station Allozyme	Population											
	A1 D4A	A2 D9	A3 D2A	A8 D11	B1 D73	Ca1a D24	Ca1 D25	Ca1 D26	Ca1 D28	Ca1 D46	Ca8 D77	Ca8 D77(hybrid)
ADH	4	4	5	2	4	6	15	8	8	8		4
1							.033					
2							.033		.063			
3	.875	1.000	1.000	1.000	1.000	1.000	.933	1.000	.938	1.000		1.000
4	.125											
ALKP	6	10	12	23	19	20	79	57	53	44	21	13
2								.018		.023		.038
3	.333	.400	.375		.237	.925	.082	.070	.047	.136	.571	.500
4	.583	.450	.375	1.000	.553	.075	.418	.518	.396	.375	.095	.038
5	.083	.150	.250		.211		.494	.395	.557	.443	.333	.423
6							.006			.023		
AAT1	6	6	11	9	2	6	52	12	8	8		2
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000
AAT2	6	6	11	9	2	6	52	12	8	8		2
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000
ENO	8	6	6	9	5	8	35	12	8	8		4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000
EST1	6	6	11	22	17	20	76	57	53	44	22	11
1			.182	.045								
2	1.000	1.000	.818	.568	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
3				.023								
5				.364								
EST2	6	6	11	27	17	20	76	57	53	44	22	11
2				.019								
3	1.000	1.000	1.000	.981	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST3	6	6	11	28	17	20	76	57	53	44	22	11
1				.018				.018				
2			.091						.142	.273		
3	1.000	1.000	.909	.982	1.000	1.000	.934	.982	.840	.727	1.000	1.000
4									.019			
5							.066					
FH	6	6	9	8	4	6	37	12	8	8	1	
1				.625								
2	1.000	1.000	1.000	.375	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
GAL	6	6	6	32	19	6	36	24	20	20	1	
1				.031				.083				
2	1.000	1.000	1.000	.969	1.000			.917	1.000	1.000	1.000	
3						1.000						
GPD	6	6	10	8	4	6	38	12	8	8	1	
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
GPI	6	6	6	28	18	22	82	57	53	44	21	17
1					.056				.009			
2	.500	1.000			.444			.012	.079	.689	.659	
3	.250							.171				
4	.167		1.000	1.000	.500	1.000	.817	.912	.311	.341	1.000	1.000
5	.083											
HK	6	6	6	8	4	6	41	12	8	8		
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
HBDH	8	6	6	28	18	8	44	12	8	8		6
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000
IDH1	6	6	10	8	4	20	83	57	53	44	22	11
1											.045	.091
3	1.000	1.000	1.000	1.000	1.000	1.000	.970	1.000	1.000	1.000	.955	.909
4							.030					

Spring Station Allozyme	Population											
	Ca9 D64	Cb2 D51	Cb2 D52	Cc1 D59	Cc3 D61	Cd1 D40	Cd1 D43	Cd1 D41	Cd1 D42	Cd2 D80	Cd2(hybrid) D80	Cd8 D72
ADH	6	10	5	4	4	7	6	4	4	4	4	4
2			.100		.125					.125	.125	
3	1.000	1.000	.700	1.000	.875	1.000	.917	1.000	1.000	.875	.875	1.000
4			.200				.083					
ALKP	51	14	9	10	7	12	10	10	5	5	4	8
2			.167		.071	.083	.050					
3		.214	.111		.429	.208	.250	.100	.200			
4	.235	.679	.500	.600		.208	.300	.650	.200	.300	.625	.938
5	.765	.107	.222	.400	.500	.500	.400	.250	.600	.700	.375	.063
AAT1	6	14	7	6	9	9	8	10	4	3	6	
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
AAT2	6	14	7	6	9	9	8	10	4	3	6	
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
ENO	9	14	6	6	4	7	8	6	4	4	4	6
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST1	51	12	5	6	9	7	6	10	4	9	15	4
1		.083	.200				.167					
2	.980	.917	.800	1.000	1.000	1.000	.833	1.000	1.000	1.000	1.000	1.000
3	.020											
EST2	51	12	5	6	9	7	6	10	4	9	15	4
2		.083										.125
3	1.000	.917	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.875
EST3	51	12	5	6	9	7	6	10	4	9	15	4
1						.214	.500		.500			
2							.083				.067	.125
3	1.000	1.000	1.000	1.000	1.000	.571	.417	1.000	.500	1.000	.933	.875
4						.214						
FH	6	12	5	6	9	9	6	6	4		3	6
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
GAL	18	12	5	6	9	9	6	6	4	9	15	6
1											.067	
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.933	1.000
GPD	6	14	6	6	9	9	8	8	4		3	6
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
GPI	54	12	6	6	4	7	6	6	4	13	17	4
2		.083				1.000	.583		.500	.038	.059	.625
3				.333				.333				
4	1.000	.917	1.000	.667	1.000		.417	.667	.500	.962	.941	.375
HK	6	14	6	6	9	9	8	6	4	3	6	
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000	1.000
HBDH	9	12	6	6	4	7	6	6	4	13	16	4
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH1	51	14	6	6	9	9	8	8	4		3	6
2											.167	
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.833	1.000	
IDH2	51	14	6	6	9	9	8	8	4		3	6
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	
LAL	50	14	6	6	9	9	8	6	4	9	15	6
1							.125					
2	1.000	1.000	1.000	1.000	1.000	1.000	.750	1.000	.875	1.000	.967	1.000
3							.125		.125		.033	
LAP	51	20	11	6	9	16	14	12	8	7	13	10
2	.961	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.500	.950
3	.039										.500	.050

Spring Station Allozyme	Population											
	A1 D4A	A2 D9	A3 D2A	A8 D11	B1 D73	Ca1a D24	Ca1 D25	Ca1 D26	Ca1 D28	Ca1 D46	Ca8 D77	Ca8 D77(hybrid)
LGG1	51	18	10	6	5	16	12	8	8	9	15	6
1	.980	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2	.020											
LGG2	21	14	7	6	5	9	10	9	4	7	13	8
1			.143				.100	.056			.077	
2	.071	.429	.286	.250		.222	.050	.167			.115	1.000
3	.405	.107			.100	.778	.200	.167		.625	.231	
4	.024	.036					.500			.125	.500	
5	.476	.321	.429	.583	.700		.150	.611	.250	.286		
6	.024	.107	.143	.167	.200					.143	.077	
MDH1	54	12	6	6	4	7	6	6	4	13	16	4
1		.042	.333									
2	1.000	.958	.667	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MDH2	54	12	6	6	4	7	6	6	4	13	16	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI1	9	12	6	6	4	7	6	6	4	4	4	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI2	9	12	6	6	4	7	6	6	4	4	4	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PPR	54	12	6	6	4	7	6	6	4	4	4	2
3	1.000	.833	.833	.750	1.000	.857	.750	1.000	.875	1.000	1.000	1.000
4		.167	.167	.250		.143	.250		.125			
PGD	54	12	6	6	4	7	6	6	4	13	16	4
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PGM1	54	12	6	6	4	7	6	6	4	13	16	4
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PGM2	54	12	6	6	4	7	6	6	4	13	16	4
2	.565	.917	1.000	1.000	.625	.786	1.000	.667	.875	.885	.875	1.000
3	.435	.083			.375	.214		.333	.125	.115	.125	
SDH1	6	14	8	4	10	16	10	8	8	6	14	10
1		.357	.188	.375	.500	.563	.600	.438	.500	.333	.179	
2	1.000	.643	.813	.625	.500	.438	.400	.563	.500	.667	.821	1.000
SDH2	6	14	8	4	11	16	10	8	8	6	14	10
1	.250	.143		.375	.045			.125		.417	.571	.350
2	.750	.857	1.000	.625	.955	1.000	1.000	.875	1.000	.583	.429	.650
TPI	9	12	6	6	4	7	6	6	4	4	4	4
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
UPDG	3	8	4	4	9	9	4	6	4		2	6
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		1.000	1.000

Table 8. Gene frequency data for *Dalhousia harrisi*. The number of individuals follow the locus name.

Spring Station Allozyme	Population											
	A1 D4	A2 D9	A3 D2A	A6 D10	A8 D11	B1 D73	B2 D74	Ca1 D25	Ca2 D78	Ca3 D76	Ca5 D75	Ca7 D34
ADH	4	4	6	6	2	1	4	4	4	8	6	4
2											.333	
3	.875	.875	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.667	1.000
4	.125	.125										
ALKP	30	32	6	29	5	13	14	45	55	48	54	52
2									.018			
3		.016		.138		.154	.179	.056	.591	.021	.389	.019
4	.967	.984	1.000	.845	1.000	.692	.821	.422	.200	.833	.370	.971
5	.033					.154		.489	.191	.135	.231	.010
6								.033		.010		
7				.017							.009	
AAT1	6	6	5	6	3	4	12	9	8	8	9	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
AAT2	6	6	5	6	3	4	12	9	8	8	9	4
1						.125						
2	1.000	1.000	1.000	1.000	1.000	.875	1.000	1.000	1.000	1.000	1.000	1.000
ENO	4	4	6	4	3	3	8	8	6	10	6	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST1	26	30	5	25	6	12	10	49	51	46	53	50
1	.442	.233	.900	.180			.250					
2	.558	.767	.100	.820	.833	1.000	.750	1.000	1.000	1.000	1.000	1.000
5					.167							
EST2	26	30	5	25	4	12	10	49	51	46	53	50
2					1.000			.010	.039	.043		
3	1.000	.967	1.000	1.000	1.000	1.000	.990	.961	.957	1.000	1.000	
4		.033										
EST3	26	30	5	25	7	12	10	49	51	46	53	50
1	.019	.017		.040								
2				.040	.071			.010		.174		
3	.981	.983	1.000	.900	.929	1.000	1.000	.990	1.000	.826	1.000	1.000
4				.020								
FH	26	30	5	23	4	3	8	9	6	8	31	4
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GAL	26	30	5	25	8	11	8	9	6	8	33	4
1	.019	.033										
2	.981	.967	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPD	28	32	5	25	4	3	10	9	6	8	33	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPI	26	30	6	25	7	12	10	48	51	48	52	50
2									.010		.010	
3						.083			.375			
4	1.000	1.000	1.000	1.000	1.000	.917	1.000	.625	.990	1.000	.990	1.000
HK	6	6	5	6	2	3	6	9	6	8	9	4
2	1.000	1.000	1.000	1.000	1.000	.667	1.000	1.000	1.000	1.000	1.000	1.000
3						.333						
HBDH	26	30	6	25	7	12	8	8	6	8	32	4
1						.708	.875					
2	1.000	1.000	1.000	1.000	1.000	.292	.125	1.000	1.000	1.000	1.000	1.000
IDH1	6	6	5	6	4	3	8	49	51	48	29	50
1								.041				
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.949	1.000	.958	1.000	1.000
4								.010		.042		

Spring Station Allozyme	Population											
	Cd1 D40	Cd2 D80	Cd3 D79	Cd5 D63	Cd9 D71	Da1 D56	Da2 D45	Da3 D44	Db1 D31	Db2 D20	Db4 D29A	E1 D6
ADH	5	2	3	6	4	2	4	7	4	4	4	6
2										.750		
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.250	1.000	1.000
ALKP	7	17	8	5	10	8	28	12	8	10	6	24
3	.357				.300	.063		.083		.300		
4	.429	.559	.875	1.000	.700	.938	1.000	.917	1.000	.700	1.000	.688
5	.214	.412	.125									.313
6		.029										
AAT1	6	3	6	5	8	6	6	12	6	10	6	10
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
AAT2	6	3	6	5	8	6	6	12	6	10	6	10
1			.167									
2	1.000	1.000	.833	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
ENO	9	2	5	6	6	6	4	11	6	8	6	8
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST1	9	32	6	5	6	6	26	12	6	10	6	28
1	.111											
2	.889	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST2	9	32	6	5	6	6	26	12	6	10	6	28
1					.167							
2	.111				.833				.300			
3	.889	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.700	1.000	1.000	
EST3	9	32	6	5	6	6	26	12	6	10	6	28
1												.036
2	.111			.300						.100		
3	.889	.969	1.000	.700	1.000	1.000	1.000	1.000	1.000	.900	1.000	.964
6		.031										
FH	4	3	6	5	6	6	6	12	6	10	6	26
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GAL	6	32	5	5	6	6	30	12	6	10	6	28
1		.031		.900		.667	.517			.800		.107
2	1.000	.969	1.000	.100	1.000	.333	.483	1.000	1.000	.200	1.000	.893
GPD	6	3	6	5	6	6	6	12	6	10	6	28
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPI	7	30	5	8	6	6	26	11	6	10	6	26
2	.143	.133		.063				.136				
3			.300	.125		.833	.538		.167	.300	.083	
4	.857	.867	.700	.813	1.000	.167	.462	.864	.833	.700	.917	1.000
HK	6	3	5	5	6	6	6	12	6	6	6	6
2	1.000	1.000	1.000	1.000	1.000	.833	1.000	1.000	.667	1.000	1.000	1.000
3						.167			.333			
HBDH	7	31	5	6	6	6	26	11	6	10	6	28
1												.196
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.804
IDH1	6	3	6	5	6	6	6	12	6	10	6	8
2		.167										.125
3	1.000	.833	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.875
IDH2	6	3	6	5	6	6	6	12	6	10	6	8
1												.125
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.875
LAL	6	32	5	5	6	6	26	12	6	10	6	28
1	.167											
2	.833	.969	.700	.800	1.000	.917	1.000	.667	.833	.700	.667	1.000
3		.031	.300	.200		.083		.333	.167	.300	.333	

Spring Station Allozyme	Population											
	E2 D7	E5 D8	E7 D17A	E8 D18	F1 D54	F2 D55	Ga2 D5A	Ga3 D14	Ga4 D12	Ga6 D16	H1 D1	H3 D19
ADH	4	8	4	6	4	4	6	16	6	8	4	6
2						.125						.250
3	1.000	1.000	1.000	1.000	1.000	.750	1.000	1.000	1.000	1.000		.333
4						.125					1.000	.417
ALKP	10	38	22	34	32	29	29	36	26	19	30	25
3		.013	.023		.031	.034	.034			.132		
4	.850	.987	.977	1.000	.969	.948	.914	.986	1.000	.816	1.000	1.000
5	.150					.017	.052	.014		.053		
AAT1	10	14	10	10	8	8	10	20	6	21	8	7
1	1.000	1.000	1.000	1.000	1.000	1.000	.950	1.000	1.000	.952	1.000	1.000
2							.050			.048		
AAT2	10	14	10	10	8	8	10	20	6	21	8	7
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
ENO	8	12	8	6	8	6	10	20	6	18	8	10
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST1	10	28	24	30	28	25	34	38	26	21	28	23
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST2	10	26	22	28	28	25	34	38	26	21	26	23
1									.013			
2		.962	.068	.179	.714		.941	.842	.481	.333	.500	.370
3	1.000	.038	.932	.821	.286	1.000	.059	.145	.519	.667	.500	.630
EST3	10	28	24	30	28	25	34	38	26	21	28	23
1			.042									.022
2		.036			.018				.019			
3	.900	.964	.958	1.000	.982	1.000	1.000	1.000	.981	.976	1.000	.978
4										.024		
7	.100											
FH	8	26	20	28	28	8	34	40	26	21	27	7
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GAL	8	26	26	26	28	29	36	42	28	21	25	27
1	.063		.712	.038	.875	.724					.120	.778
2	.938	1.000	.288	.962	.125	.276	1.000	1.000	1.000	1.000	.880	.222
GPD	10	30	24	30	28	8	36	42	28	21	27	7
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPI	10	30	24	30	28	25	36	42	28	21	26	28
3	.450	.017	.021			.060						.268
4	.550	.983	.979	1.000	1.000	.940	1.000	1.000	1.000	1.000	1.000	.732
HK	6	10	6	6	6	6	10	20	6	18	6	5
1										.028		
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.972	1.000	1.000
HBDH	10	28	24	28	28	25	36	42	28	21	28	28
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH1	8	12	8	8	8	8	10	20	6	21	7	7
3	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH2	8	12	8	8	8	8	10	20	6	21	7	7
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
LAL	8	28	22	28	28	25	36	42	28	21	27	25
1											.037	
2	.875	1.000	1.000	1.000	1.000	1.000	.917	1.000	1.000	.762	.963	1.000
3	.125						.083			.238		
LAP	8	36	22	32	28	25	36	42	28	23	27	25
2	.063							.024		.043		
3	.938	1.000	1.000	1.000	1.000	.980	.972	.976	1.000	.957	1.000	1.000
4						.020	.028					

Table 9. Gene frequency data for *Fluvidona centralia*. The number of individuals follow the locus name.

Spring Station Allozyme	Population						
	Cd11 D70	E1 D62	E3 D23(A+B)	F9 D53	Ga1 D13	Ga2 D5B	Ga6 D15
AAT1	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
AAT2	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
ALKP	4	12	10	8	12	12	4
1						.167	
2	1.000	1.000	1.000	1.000	.417	.708	1.000
3					.583	.125	
ENO	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST1	3	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST2	1	8	8	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	.875	1.000
2						.125	
EST3	1	8	8	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPI	4	12	12	8	12	12	4
1							
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPT1	4	12	16	12	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
GPT2	4	12	16	12	12	12	4
1	1.000	1.000		1.000			
2			1.000		1.000	1.000	1.000
GPD	4	12	16	12	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
HBDH	4	12	12	8	12	12	4
1	.750						
2	.250	1.000	1.000	1.000	1.000	1.000	1.000
IDH1	4	12	16	12	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
IDH2	4	12	16	12	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MDH1	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MDH2	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
MPI	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PPR	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
PGM1	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	1.000	1.000	1.000
2							
PGM2	4	12	12	8	12	12	4
1							
2	1.000	1.000	1.000	1.000	1.000	1.000	1.000
3							
6PGD	4	12	12	8	12	12	4
1	1.000	1.000	1.000	1.000	.250	.417	1.000
2					.750	.583	

